ECOLOGY

Vol. 35 OCTOBER, 1954 No. 4

COMPARISON OF LINE INTERCEPTION AND POINT CONTACT METHODS IN THE ANALYSIS OF MIXED GRASS RANGE VEGETATION[1]

WARREN C. WHITMAN AND EINAR I. SIGGEIRSSON[2]
North Dakota Agricultural Experiment Station, Fargo, North Dakota
and
Iceland School of Agriculture, Holar i Hjaltadal, Iceland

INTRODUCTION

Two methods of sampling range vegetation for the determination of botanical composition and density which have shown particular promise for use in research studies are the line interception method of Canfield (1941) and the point contact method or point quadrat originally developed by Levy and Madden (1933). The line interception method in addition to its development and use by Canfield (1941, 1950) has been tested by Anderson (1942) in tall grass prairie vegetation, Parker and Savage (1944) on sand dune-sage vegetation in the Southern Great Plains, and by Hormay (1949) on bunchgrass types in California. It is currently being used in a number of range research studies.

The point contact method has been used extensively in New Zealand and Australia (Crocker and Tiver 1948) and has been used in the determination of the composition and density of short grass and mixed grass range types in Canada by Clarke, Campbell, and Campbell (1942) and Coupland (1950). An early test of the method on a mixed grass range type in western North Dakota was made by Hanson (1934). Numerous tests of the method on tame pastures have been made in this country by such workers as Tinney, Aamodt, and Ahlgren (1937), Arny and Schmid (1942), Arny (1944), Drew (1944), and others.

The purposes of this study were to compare line interception and point contact methods as to field adaptability and differences in density and composition evaluation of mixed grass range; to assess the variability of species density in the native vegetation; and to secure an estimate of the number of sample units of each method needed to provide reliable statistical information on species density populations in range vegetation of this type.

[1] Published with the approval of the Director, North Dakota Agricultural Experiment Station.

[2] Formerly Instructor of Agronomy, Iceland School of Agriculture.

METHODS

An apparently uniform piece of upland, native, ungrazed mixed grass range at the Dickinson Experiment Station in southwestern North Dakota was chosen for this study. The principal species in the cover were needle-and-thread (*Stipa comata* Trin. and Rupr.), blue grama grass (*Bouteloua gracilis* (HBK.) Lag.), threadleaf sedge (*Carex filifolia* Nutt.), needle-leaf sedge (*Carex eleocharis* Bailey), western wheatgrass (*Agropyron smithii* Rydb.), and plains reedgrass (*Calamagrostis montanensis* Scribn.). The principal miscellaneous grasses were prairie June grass (*Koeleria cristata* (L.) Pers.) and green needlegrass (*Stipa viridula* Trin). A number of forbs were present, though in relatively low numbers, the most important being scarlet globemallow (*Sphaeralcea coccinea* (Pursh) Rydb.), western wallflower (*Erysimum asperum* (Nutt.) DC.), and skeleton weed (*Lygodesmia juncea* (Pursh) Don). No shrubs were present on the area.

The field work in this study was done in late July and August of 1948. Grass was nearly mature at this time and was, in general, in somewhat better over-all condition than average.

The experimental plot of native range vegetation was laid out in a rectangle 300 feet wide and 500 feet long, having a total area of slightly less than 3.5 acres. This sampling area was then divided into 15 major plots, each 100 feet by 100 feet, with each of these plots subdivided into two minor plots each 50 x 100 feet. To each of these minor plots was then assigned four line transects and ten point frame units (100 points). Within each 50 x 100 foot plot, the location of line transects and point sets were determined by random selection, using an imaginary grid with a 2.5 foot interval. For the area as a whole 120 line transects were taken and 300 point sets, or a total of 3,000 points, for each of the two point contact analyses.

In the line interception method, a ten-meter line with intercepts measured to the nearest half-centimeter was used following the modifications of Parker and Savage (1944). The line was given a width of one centimeter, *i.e.*, one-half centimeter, on either side of the wire. An arbitrary value of one centimeter was allowed for the intercept of all single-stalked species. Since there were no shrubs on the area, their measurement posed no problem.

The point apparatus used was a wooden frame with the pins held in the inclined position at an angle of 45° to the vertical, as used by Tinney, Aamodt, and Ahlgren (1937). Pins were spaced two inches apart on the frame. The point contact method was used in two ways with a separate analysis of the vegetation being made by each system.

The first system of using the point contact method is here designated the "all-contacts" system. In this system all contacts of the point with the vegetation as the pin is projected downward are recorded by species, irrespective of the number of times any species is hit. If, at ground level, the point hits bare ground rather than vegetation, bare ground is recorded, even though aerial contacts have been recorded for the point in its projection through the overlying vegetation. Species density is calculated by expressing the number of hits on any one species per 100 points as a percentage of the total number of vegetation hits per 100 points and multiplying this by 100 minus the percentage of bare ground.

In the second system, here designated the "basal-contact" system, only basal contacts of vegetation are recorded. A plant is hit when the point of a pin touches its base. Hits for each species are recorded and results are expressed in terms of the percentage of hits per 100 points. This is essentially the manner in which the point contact method has been used by Clark *et al.* (1942).

In the statistical analysis of the data, four line transects and ten point sets (100 points) were considered to constitute a sample. Statistical procedures followed are those of Snedecor (1940). Calculations of the number of sampling units needed for different degrees of precision using each of the methods are based on the procedures of Costello and Klipple (1939) and Canfield (1950).

General Differences in Vegetation Analysis

The data of Table I show that there were some substantial differences in evaluation of species density and percentage composition of the vegetation as determined by the line interception method and the two variations of the point contact method.

Table I. *Average percentage density and percentage composition of mixed grass range vegetation on the study area as determined by line interception and point contact methods*

Species	Density-Per cent			Composition-Per cent		
	Line intercept.	Point contact		Line intercept.	Point contact	
		All-contacts	Basal-contact		All-contacts	Basal-contact
Needle-and-thread	5.40	9.51	7.66	26.09	29.79	24.49
Blue grama grass	5.84	7.33	12.40	28.21	22.96	39.64
Western wheatgrass	1.28	3.17	1.50	6.18	9.93	4.80
Plains reedgrass	0.73	1.03	0.43	3.53	3.23	1.37
Miscellaneous grasses	1.39	1.89	1.76	6.71	5.93	5.63
Sedges	4.33	6.06	4.43	20.92	18.98	14.16
Forbs	1.73	2.93	3.10	8.36	9.18	9.91
Totals	20.70	31.92	31.28	100.00	100.00	100.00

In the presentation of the data needle-and-thread, blue grama grass, western wheatgrass, and plains reedgrass are given separate consideration, while the species comprising the miscellaneous grasses, the sedges, and the forbs have been lumped into composite groups.

With the line interception estimates taken as a standard, the all-contacts system provided an appreciably higher estimate of density of all species, composite groups, and total density, while the basal-contact system provided appreciably higher estimates only in needle-and-thread, blue grama grass, forbs, and total density. The most striking difference between the line interception and the point contact methods is the much higher evaluation that the point contact methods put on total density. The total density of the vegetation by the point contact method is approximately 50 per cent greater than that indicated by the line interception method. Another outstanding difference is shown by the high density evaluation of blue grama grass by the basal-contact method. The estimate of density of this species by the basal-contact method, 12.40 per cent, is over twice the estimate provided by the line interception method, and 69 per cent greater than the blue grama density estimate by the all-contacts method.

When the density values are converted to percentage composition, it is apparent that the high density estimate of blue grama grass by the basal-contact system results in an estimate of percentage composition by this method that is substantially different from the estimates provided by the other two methods. By the basal-contact system, blue grama grass makes up 39.64 per cent of the vegetation, while it makes up only 22.96 per cent by the all-contacts system, and 28.21 per cent by the line interception method. Each method actually provides a somewhat different estimate of per-

centage composition of the vegetation on the study area. The fact that each of the three methods provides a different estimate of density and percentage composition serves to emphasize that caution should be used in making comparisons between studies in which different methods of vegetation analysis have been used.

Application of the "t" test shows that between the line interception method and the two variations of the point contact method, differences in density evaluations are significant beyond the one per cent level for needle-and-thread, blue grama grass, forbs, and total density. Differences for plains reedgrass and miscellaneous grasses are not significant. In the comparison, line interception by all-contacts, differences in density evaluations are also significant beyond the one per cent level for western wheatgrass and the sedges. Line interception by basal-contact shows no significant difference between the two methods in the density evaluation of western wheatgrass and the sedges. Differences in density of needle-and-thread, blue grama grass, and sedges are significant beyond one per cent in the comparison, all-contacts by basal-contact; all other differences in this comparison are not significant.

At the intensities of sampling used, the methods were not equally efficient in indicating the presence of the different species. A total of 57 species was found on the study area. Thirteen of these species were grasses, three were sedges, and 41 were forbs. The line interception method picked up 51 species, of which 12 were grasses and three were sedges. The all-contacts method indicated the presence of 49 species, including 11 grasses and three sedges. The basal-contact method was notably poorer in indicating species presence. Only 22 species were picked up by his method, seven of the species being grasses and three being sedges. However, all species present in any appreciable abundance were recorded by this method.

Variability and Sampling Errors

The high degree of natural variability in density and composition of native, mixed grass range vegetation has been noted by Hanson (1934). Pechanec and Stewart (1941) studied population variability in sagebrush-grass range and found it to be two to three times greater than that normally encountered in experiments on cultivated land. The variability of species density on the study area, as shown in Table II, was in the same general range as that reported by these investigators.

Needle-and-thread, blue grama grass, and the sedges (composite of three *Carex* species), are the most important components of the vegetation on the area, making up over 70 per cent of the vegetation as determined by each of the methods (Table I). All of these have coefficients of variability in excess of 30 per cent of the mean species or group density.

Table II. *Standard deviations and coefficients of variability for species, groups, and total density as calculated from data provided by line interception and point contact analyses of mixed grass range*

Species	Line interception		Point contact			
			All-contacts		Basal-contact	
	Standard deviation—% density	Coefficient of variability—%	Standard deviation—% density	Coefficient of variability—%	Standard deviation—% density	Coefficient of variability—%
Needle-and-thread	2.08	39	3.14	33	2.54	33
Blue grama grass	2.32	40	2.61	36	6.20	50
Western wheatgrass	1.21	95	1.19	38	0.80	53
Plains reedgrass	1.06	145	0.86	83	0.74	172
Miscellaneous grasses	1.05	76	1.06	56	1.58	90
Sedges	2.02	47	2.24	37	2.62	59
Forbs	1.12	65	1.26	43	2.69	87
Total density	3.99	13	7.52	24	7.37	23

Plains reedgrass, the species of lowest mean density that is here given separate consideration, shows a coefficient of variability of 145 per cent by the line interception method, 83 per cent by the all-contacts method and 172 per cent by the basal-contact method. Total density, as might be expected, shows less variability than any of the individual species or composite groups, the variability by the line interception method being 13 per cent of mean total density, 24 per cent by the all-contacts method, and 23 per cent by the basal-contact method.

It is interesting to note that, with the exception of total density, the coefficients of variability for all species and groups as estimated by the all-contacts method are appreciably lower than the variability estimates provided by the line interception method. The estimates of variability by the basal-contact method are lower than those by the line interception method only for needle-and-thread and western wheatgrass. The estimate of variability for density of needle-and-thread is the the same by both variations of the point contact method, and approximately the same for total density, but otherwise the estimates of variability by the all-contacts method are substantially lower than the estimates provided by the basal-contacts method.

Apparently the generally lower variability estimates afforded by the all-contacts method are related to the fact that the inclusion of aerial contacts in the individual observation by the all-contacts method results in indicating the presence and

relative abundance of a species, even though no basal area may be occupied by that species at the particular point of observation.

In vegetation as variable as that found on the study area, it would be expected that rather high intensity of sampling would be needed to produce reasonably precise estimates of species density population means. Table III gives the standard errors and sampling errors (standard error as percentage of the mean) for species density and total density as calculated from the data provided by the line interception and point contact analyses of the vegetation on the study plot.

TABLE III. *Standard errors of means and sampling errors (standard error as percentage of mean) as calculated from data provided by line interception and point contact analyses of mixed grass range*

Species	Line interception		Point contact			
			All-contacts		Basal-contact	
	Standard error—% density	Sampling error—%	Standard error—% density	Sampling error—%	Standard error—% density	Sampling error—%
Needle-and-thread	0.19	4	0.57	6	0.46	6
Blue grama grass	0.21	4	0.48	7	1.13	9
Western wheatgrass	0.11	9	0.22	7	0.15	10
Plains reedgrass	0.10	14	0.16	16	0.14	33
Miscellaneous grasses	0.10	7	0.19	10	0.29	17
Sedges	0.18	4	0.41	7	0.48	11
Forbs	0.10	6	0.23	8	0.49	16
Total density	0.36	2	1.37	5	1.35	5

With the intensities of sampling used in this study, sampling errors for total density and density of all species and groups, with the exception of plains reedgrass, were under 10 per cent of the means as determined by the line interception method. By the all-contacts method, sampling errors were 10 per cent or less for all species and groups except plains reedgrass, which had a sampling error of 16 per cent. By the basal-contact method only needle-and-thread, blue grama grass, western wheatgrass, and total density had sampling errors of 10 per cent or less.

The line interception method provided sampling errors of less than 5 per cent for needle-and-thread, blue grama grass, the sedges, and total density. The two variations of the point contact method provided sampling errors of 5 per cent or less only for total density. It should be borne in mind that while the intensity of sampling is the same for the all-contacts and basal-contact methods (3,000 points), this intensity is not necessarily equal to the sampling intensity used with the line interception method (120 line transects). Obviously 3,000 points in the point contact methods do not yield estimates for all species and groups equal in precision to those obtained from 120 line transects.

Numbers of Observations Required for Equal Precision

Estimates have been made of the number of individual observations required for the different methods to yield species density estimates of equal precision, *i.e.*, standard errors of the same magnitude in relation to the means. The numbers of observations needed to produce sampling errors of 5 per cent and 10 per cent of the means have been calculated for each method, using the transposed formula for the standard error of a mean.[3] The calculated values for number of observations are given in Table IV. These values are at the 68 per cent level of probability. At this level the odds are 2 to 1 that repeated samplings, by the same methods and with the same number of observations, would not result in the occurrence of errors larger than those specified.[4]

The data of Table IV show that very large numbers of observations are needed at 5 per cent accuracy, if all species and groups are to be sampled to the same degree. While it would not be

TABLE IV. *Numbers of line transects and numbers of points required with the line interception and point contact methods to produce sampling errors of 5 per cent and 10 per cent of means; calculated at 68 per cent level of probability*

Species	Standard error 5% of mean			Standard error 10% of mean		
	Line interception	All-contacts	Basal-contact	Line interception	All-contacts	Basal-contact
Needle-and-thread	62	4,300	4,600	15	1,100	1,100
Blue grama grass	67	4,900	10,100	16	1,300	2,500
Western wheatgrass	407	5,500	10,000	87	1,500	2,800
Plains reedgrass	700	29,600	137,500	224	7,400	34,400
Miscellaneous grasses	220	14,000	31,300	55	3,100	7,800
Sedges	85	5,600	14,300	23	1,400	3,600
Forbs	156	6,900	27,900	43	1,900	7,600
Total density	15	2,300	2,200	4	600	600

[3] $N = \frac{S^2}{(S\bar{x})^2}$ The standard deviation derived from the plot data is used for S, and 5% or 10% of the mean density of any particular species or group is substituted for $S\bar{x}$.

[4] No discussion of the possibility of sampling to secure sampling errors of 5% and 10% of the mean at the 5% level of probability (odds 19 to 1) has been included. An approximation of the number of samples needed at this level of probability may be obtained by multiplying the figures given in Table IV by 4 (approximate value of t^2 at the appropriate number of degrees of freedom). It is apparent that even for such species as blue grama grass and the sedges, sampling at this intensity is a virtual impossibility.

impossible to sample at 5 per cent accuracy for all species and groups, it would be impractical to attempt it. To sample at 5 per cent accuracy for the three principal species and groups—needle-and-thread, blue grama grass, and the sedges—would require 85 line transects, 5,600 all-contacts points, or 14,300 basal-contact points. If 85 line transects were used this would provide 5 per cent accuracy for the sedges and better than 5 per cent accuracy for needle-and-thread and blue grama grass. Only on western wheatgrass and plains reedgrass would the degree of accuracy be beyond 10 per cent.

With 5,600 all-contacts points, sampling errors for needle-and-thread, blue grama grass, western wheatgrass, and the sedges would all be 5 per cent or under. Only plains reedgrass would have a sampling error greater than 10 per cent. Using the basal-contact method, 14,300 points would meet the 5 per cent requirements for the three major components plus western wheatgrass. The sampling error for plains reedgrass would again be greater than 10 per cent.

This level of sampling would still be rather high for most studies, particularly for those studies in which it was desired to sample a number of subtypes in a survey of density and composition. It would not be too difficult to sample for the three major components of the vegetation at the 10 per cent level with any of the three methods. This would require 23 line transects, 1,400 all-contacts points, or 3,600 basal-contact points. In fact these figures might well be taken as a reasonable minimum working basis for the use of any of these three methods in the analysis of vegetation of this type and density.

One advantage that has been claimed for the point contact method is that it is more rapid than most other reliable quantitative methods. No careful study of time requirements has been made in this work, but it was apparent in the course of the study that when employed to secure equal degrees of precision in density estimates of the three major components of the vegetation, the point contact methods were not much more rapid than the line interception method.

The all-contacts variation of the point method does have an advantage over the line interception method in the analysis of the single-stalked species, which were present in minor amounts in the vegetation on the study area. Apparently it also has this advantage, in part at least, over the basal-contact method. Practical field working rates for two men in vegetation of this type, density, and growth condition were found to be about 20 line transects, 1,500 all-contact points, or 3,000 basal-contact points per day. Thus an analysis of the vegetation requiring 10 per cent accuracy for western wheatgrass would take about four days for two men using the line interception method, and only about a day by either of the point contact methods. On the same basis, an analysis requiring 10 per cent accuracy for plains reedgrass would take about 11 days by the line interception method, 11 days by the basal-contact method and 5 days by the all-contacts method.

An objection that could be made to the basal-contact method is that it places a much higher valuation on the density of blue grama grass, as compared to either of the other two methods. Hanson (1934) considered that the point contact method tended to overemphasize the importance of blue grama grass and the sedges. If the line interception method is taken as the standard, then the basal contact method does seriously over-value the density of blue grama grass, although the density values for the sedges are about the same by the two methods.

There is no possible way of knowing the true density picture, except as it may be reflected by any given method of analysis. Apparently the point contact methods can be made just as reliable as the line interception method insofar as sampling errors are concerned. And when the methods are employed to gain equal precision of estimate for the principal components of this type of vegetation, they require about equal expenditure of effort. One possible exception to this should be noted; point analysis can be accomplished much more rapidly in short vegetation than in tall growing vegetation. It must be recognized that each of the methods will not give quite the same picture of the density or composition of the vegetation, because of evaluation differences inherent in the methods themselves.

Summary

A study of the evaluation of species density in mixed grass range by restricted random sampling with line interception and point contact methods has been made. It was found that the point contact methods result in over-all higher density evaluations for most species and groups than does the line interception method. Total density of plant cover was about 21 per cent by the line interception method and about 32 per cent by point contact methods.

The all-contacts variation of the point method was about equal to the line transect method in indicating the presence of species on the study area at the intensities of sampling used, but the basal-

contact variation of the point system was notably poorer in this respect. This latter method indidated only 22 species out of the total of 57 recorded for the study area, while the line interception method picked up 51 species and the all-contacts method, 49 species.

Despite the uniform appearance of the vegetation on the study area, variability in species and group densities was high. Needle-and-thread, blue grama grass, and the sedges (composite group of three *Carex* species), which made up over 70 per cent of the vegetation on the area, showed variabilities in excess of 30 per cent of their means. With the exception of needle-and-thread and total density, the coefficients of variability as estimated by the all-contacts method are appreciably lower than the variability estimates provided by the line interception and basal-contact methods.

When used to secure density estimates of equal accuracy for the major components of the vegetation, the point contact methods are not much more rapid than the line interception method. The all-contacts analysis, however, does have an advantage in this respect, especially with the single-stalked species such as western wheatgrass, plains reedgrass, and most of the forbs. The lower variability in the density estimate of these species and groups permits securing analyses of equal precision with less effort, or analyses of greater precision with the same effort.

Sampling to secure sampling errors not in excess of 5 per cent of the means at the 68 per cent level of probability for all species and composite groups, as used in this study, while not impossible, would be a task of considerable magnitude with any of the methods studied. In intensive studies where sufficient time and labor are available, it would be practical to sample the principal species at 5 per cent accuracy and the most important secondary species and groups with sampling errors not to exceed 10 per cent.

For survey work in vegetation of this type and density a minimum working basis of 23 line transects, 1,400 all-contacts points or 3,600 basal-contact points is suggested. This would provide for estimates of the three major components of the vegetation, needle-and-thread, blue grama grass, and the sedges, with sampling errors of 10 per cent or less, and all other species and groups, except plains reedgrass, with sampling errors somewhere between 10 and 20 per cent.

References

Anderson, Kling L. 1942. A comparison of line transects and permanent quadrats in evaluating composition and density of pasture vegetation of the tall grass prairie type. Jour. Amer. Soc. Agron. **34**: 805-822.

Arny, A. C. 1944. Alfalfa and grass percentage determinations with the inclined point apparatus at different stages of development of the mixtures. Jour. Amer. Soc. Agron. **36**: 996-998.

Arny, A. C., and A. R. Schmid. 1942. A study of the inclined point quadrat method of botanical analysis of pasture mixtures. Jour. Amer. Soc. Agron. **34**: 238-247.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Jour. Forestry **39**: 388-394.

———. 1950. Sampling ranges by the line interception method. Southwestern For. and Range Exp. Sta. Res. Rept. **4**, 28 p. (mimeo).

Clarke, S. E., J. A. Campbell, and J. B. Campbell. 1942. An ecological and grazing capacity study of the native grass pastures in southern Alberta, Saskatchewan and Manitoba. Dom. Can. Dept. Agr. Tech. Bull. **44**, 31 p.

Costello, D. F., and G. E. Klipple. 1939. Sampling intensity in vegetation surveys made by the square-foot density method. Jour. Amer. Soc. Agron. **31**: 800-810.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. Ecological Monog. **20**: 271-315.

Crocker, R. L., and N. S. Tiver. 1948. Survey methods in grassland ecology. Jour. Brit. Grassland Soc. **3**: 1-26.

Drew, W. B. 1944. Studies on the use of the point-quadrat method of botanical analysis of mixed pasture vegetation. Jour. Agr. Res. **69**: 289-297.

Hanson, H. C. 1935. A comparison of methods of botanical analysis of the native prairie in western North Dakota. Jour. Agr. Res. **49**: 815-842.

Hormay, A. L. 1949. Getting better records of vegetation changes with the line interception method. Jour. Range Mgt. **2**: 67-69.

Levy, E. B., and E. A. Madden. 1933. The point method of pasture analysis. New Zealand Jour. Agr. **46**: 267-279.

Parker, K. W., and D. A. Savage. 1944. Reliability of the line interception method in measuring vegetation on the Southern Great Plains. Jour. Amer. Soc. Agron. **36**: 97-110.

Pechanec, Joseph F., and George Stewart. 1941. Sagebrush-grass range sampling studies: variability of native vegetation and sampling error. Jour. Amer. Soc. Agron. **33**: 1057-1071.

Snedecor, G. W. 1940. Statistical methods. ed. 3. Iowa State College Press, Ames, Iowa.

Tinney, Fred W., O. S. Aamodt, and H. L. Ahlgren. 1937. Preliminary report of a study on methods used in botanical analyses of pasture swards. Jour. Amer. Soc. Agron. **29**: 835-840.

SMALL MAMMAL POPULATIONS ON THE ISLANDS OF BASSWOOD LAKE, MINNESOTA[1]

JAMES R. BEER, PAUL LUKENS AND DAVID OLSON
Dept. of Entomology and Economic Zoology, University of Minnesota
St. Paul, Minnesota

Islands have long been recognized as having faunas with unique properties. Beginning in 1950 the Quetico-Superior Wilderness Research Center, by giving support and making available its facilities, made it possible for us to conduct investigations on the small mammals found on the islands in Basswood Lake, Lake County, Minnesota. This paper reports on three years' work in which we have attempted to ascertain the status of the natural populations on these islands. The study was set up to determine (1) whether or not the islands of Basswood Lake would show relatively complete isolation throughout the year with water in the summer and ice in the winter serving as effective barriers to ingress and egress and (2) to determine some of the characteristics of the small mammal populations on these islands.

Basswood Lake is typical of the large lakes along the Ontario-Minnesota boundary. These lakes lie in rock-bound basins formed by the glaciers of the Pleistocene Epoch (Zumberge 1952). The upland is characterized by numerous low bedrock hills and knobs which are covered with a very thin mantle of glacial drift (Thiel 1947). Interspersed among these hills are numerous swamps and small lakes.

The original dominant vegetation of this area was composed primarily of conifers. The characteristic trees of the upland forest were the red and white pines, white spruce, balsam fir and white birch while the swamps were filled with black spruce, tamarack, white cedar and black ash. Deciduous trees such as aspen, balsam poplar, red maple, pin cherry, yellow birch and mountain ash were found throughout the area, but except where there had been some disturbance, they formed only a small part of the vegetation (Rosendahl and Butters 1928).

The present vegetation shows the effects of heavy logging, burning and reburning. The destruction of the original forest was followed by the rapid growth of aspen and white birch which, at the present time, form the dominant part of the flora. The islands, for the most part, were affected less by these destructive forces than the mainland.

[1] Paper No. 3026, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

Owing to its location this area has a markedly continental climate with its wide variations in temperature and dominantly summer rainfall. The annual rainfall is about 25 inches. While the summer heat is usually somewhat moderated in the vicinity of the large lakes the winter temperatures often fall far below freezing for considerable periods of time. The last killing frost of the spring comes about May 27 and the first of the fall about September 22 though frost may occur during any month of the year in localized areas ("Climate and Man," 1941). Snow is probably important to the small mammals since it covers the ground as an insulating blanket for about five months of the year. The lakes are normally frozen over by the middle of November and the ice does not break up until about the first of May (see Table I).

TABLE I. *Freeze-up and Break-up Dates for Basswood Lake.*

Year	Break-up	Freeze-up
1950	April 28	Nov. 17
1951	May 6	Nov. 10
1952	April 26	Nov. 19
1953	April 24	

The islands studied were selected primarily on the basis of availability to the camp area which was located on the south end of Hoist Bay (see Fig. 1). A second prerequisite was the lack of human disturbance. Islands having occupied habitations were eliminated although several of the selected islands had camp sites which were used occasionally by canoe parties. These areas varied in size from a small fraction of an acre to about 419 acres (see Table II) and in distance from the mainland from about 80 feet for island No. 11 to about 1200 feet for island No. 3 (see Fig. 1).

Twenty-one, 26 and 24 of the 32 islands were trapped in 1950, 1951 and 1952 respectively. It was not possible to use all of the islands each year due to lack of time and to their being used for other studies. Five mainland areas were chosen to give as representative as possible sample of the habitats present.

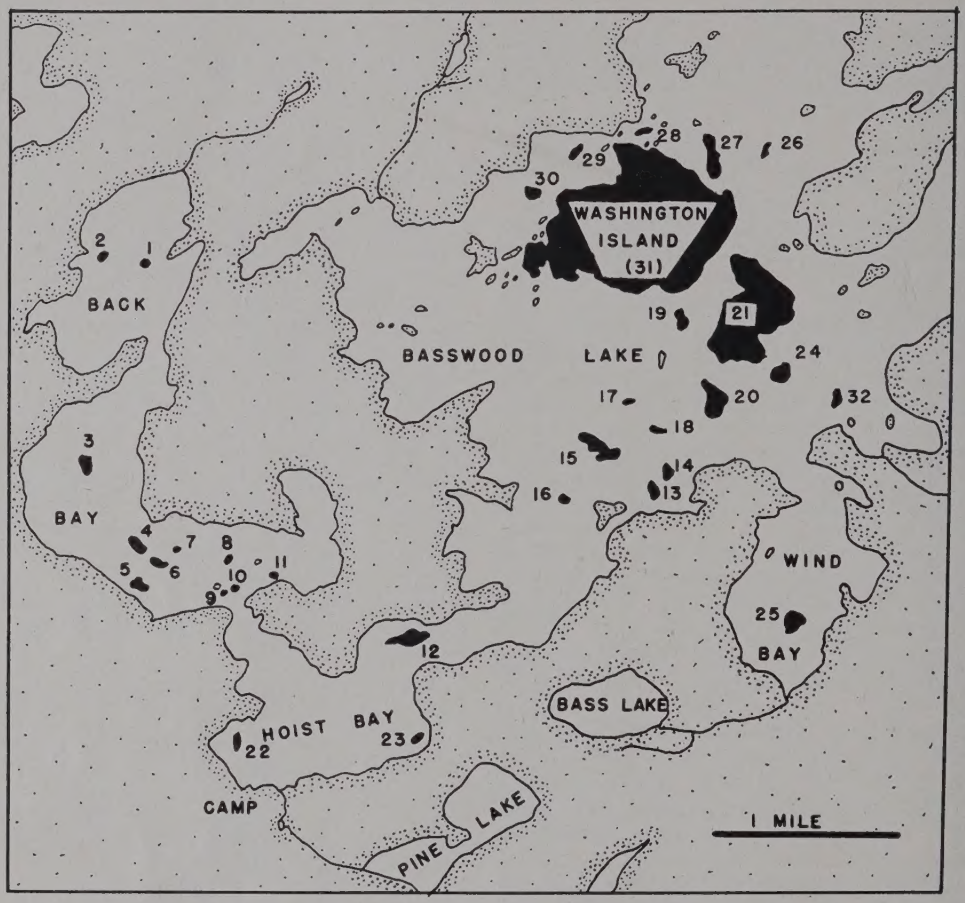

FIG. 1. Map of the Basswood Lake area showing th e islands that were studied. These islands are blocked in and numbered.

METHODS

Most of the data were obtained by the use of standard snap-type mouse traps. On the mainland and larger islands lines were set with a trap interval of 30 feet. These lines ran to a length of 50 traps or to the far shore of the island and were located with the idea of sampling all of the major habitats recognized on each island. An attempt was made to keep these lines at least 100 feet apart. This, however was not possible on the small islands. In no case were less than 10 trap days used (see Table II).

All of the trapping was carried out between the dates of June 21 and July 23. The traps were all baited with peanut butter and were placed without selection of the spot in relation to the immediate environmental conditions. In 1950 the traps were left out for but a single day in any one place. In 1951 and 1952, however, the traps were left out three days before being moved to a new location.

Live trapping, marking and releasing animals at the point of capture was used to a limited extent. Problems of transportation, and manpower limited the amount of this type of work to about 610 trap days on 4 islands. The live traps were set on a 45 foot grid on these islands. Except for those instances where the text refers explicitly to live trapping and/or tagged mice the discussion refers to the snap trapping data.

Animals larger than chipmunks were not considered in this study.

TABLE II. *Trapping Data.*

Island No.	Acres	1950*						1951						1952					
		Trap Days	Microtus	Clethrionomys	Peromyscus	Zapus	Other species	Trap Days	Microtus	Clethrionomys	Peromyscus	Zapus	Other species	Trap Days	Microtus	Clethrionomys	Peromyscus	Zapus	Other species
1	.2	15	..	..	..	..	..	75	..	..	..	..	..	96	8	..	..	..	..
2	.9	28	..	..	..	..	..	126	..	1	11	..	..	201	8	8	..	..	..
3	2.4	65	..	2	..	..	..	—	..	..	..	..	..	150	4	14	15	1	..
4	2.6	57	..	..	..	..	..	129	..	6	..	..	..	292	..	6	7	..	..
5	1.0	56	..	..	..	..	..	207	3	9	..	..	1	130	5	5	..	2	..
6	3.8	80	..	..	..	..	2	—	..	..	..	..	..	402	1	29	7	..	1
7	.1	10	..	..	..	..	..	21	..	..	..	..	..	36	1	..	..	..	..
8	.1	10	..	..	..	..	..	21	..	..	..	..	..	33	4	..	..	..	..
9	.1	12	..	..	..	..	..	—	..	..	..	..	..	30	2	..	..	..	..
10	.2	12	..	..	..	..	..	39	..	..	..	..	..	78	5	..	..	..	..
11	.2	11	..	..	..	..	..	45	..	4	..	..	..	78	1	..	4	..	..
12	9.3	143	1	..	..	7	1	—	..	..	..	..	..	—	..	..	..	..	..
13	2.2	41	..	..	..	..	..	114	..	..	3	..	..	165	11	..	7	..	..
14	4.0	56	..	..	..	..	..	117	..	..	..	..	..	180	3	2	5	..	2
15	10.7	127	..	3	..	..	..	—	..	..	..	..	..	—	..	..	..	..	..
16	.1	10	..	..	..	..	..	30	1	..	..	..	..	30	1	..	..	..	..
17	.6	15	1	..	..	..	..	78	..	..	..	..	..	72	..	..	..	..	..
18	.9	25	..	..	..	..	..	66	..	..	..	..	..	96	..	9	..	..	..
19	3.4	56	..	..	..	..	..	192	..	7	..	..	..	225	3	12	6	1	..
20	12.7	154	2	..	..	2	..	433	8	6	..	3	5	336	9	7	11	4	2
21	97.5	200	2	..	2	1	1	598	1	5	21	3	5	750	6	18	17	6	2
22	1.4	—	..	..	..	..	..	114	3	..	..	..	..	174	2	..	..	..	..
23	3.3	—	..	..	..	..	..	—	..	..	..	..	..	165	3	..	..	..	..
24	7.1	—	..	..	..	..	..	203	1	2	..	1	..	228	11	3	..	2	..
25	6.5	—	..	..	..	..	..	162	..	8	..	..	..	300	48	31	..	..	..
26	1.1	—	..	..	..	..	..	105	..	2	..	..	..	—	..	..	..	..	..
27	12.5	—	..	..	..	..	..	449	..	9	13	..	..	—	..	..	..	..	..
28	1.6	—	..	..	..	..	..	104	..	5	..	..	..	—	..	..	..	..	..
29	2.7	—	..	..	..	..	..	165	..	..	..	..	..	—	..	..	..	..	..
30	3.3	—	..	..	..	..	..	138	..	..	10	..	..	—	..	..	..	..	..
31	419.	—	..	..	..	..	..	368	2	9	37	1	..	300	16	6	21	4	..
32	3.3	—	..	..	..	..	..	159	..	15	..	1	..	—	..	..	..	..	..
Islands	1,183	5	5	2	10	4		4,258	19	88	95	9	11	4,447	152	150	100	20	7
Mainland	203	5	1	4	1	0		246	4	9	4	0	3	1,524	64	23	34	2	9
Pine Co.	..	..	..	..	..	..	..	976	15	61	15	5	3	..	..	..	..	..	..

*In 1950 the traps were left only one day at a place rather than three days as in 1951 and 1952.

RESULTS

During the period of this study nine species of small mammals were trapped. These included the meadow mouse (*Microtus pennsylvanicus*), lemming mouse (*Synaptomys cooperi*), red-backed mouse (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), meadow jumping mouse (*Zapus hudsonius*), short-tailed shrew (*Blarina brevicauda*), cinereous shrew (*Sorex cinereus*), least chipmunk (*Eutamias minimus*) and eastern chipmunk (*Tamias striatus*). With the exception of the least and eastern chipmunks all of the species found on the mainland were taken on the islands.

The status of the small mammals on these islands can best be discussed with separate consideration of the hibernating and non-hibernating species. The hibernators include the two chipmunks and the jumping mouse; and the non-hibernators the meadow mouse, lemming mouse, red-backed mouse, deer mouse and the shrews.

The trends in occupancy of the islands for the several species are shown in Fig. 2. Small mammals were found on about 28 per cent of the islands in 1950. There was a general increase in

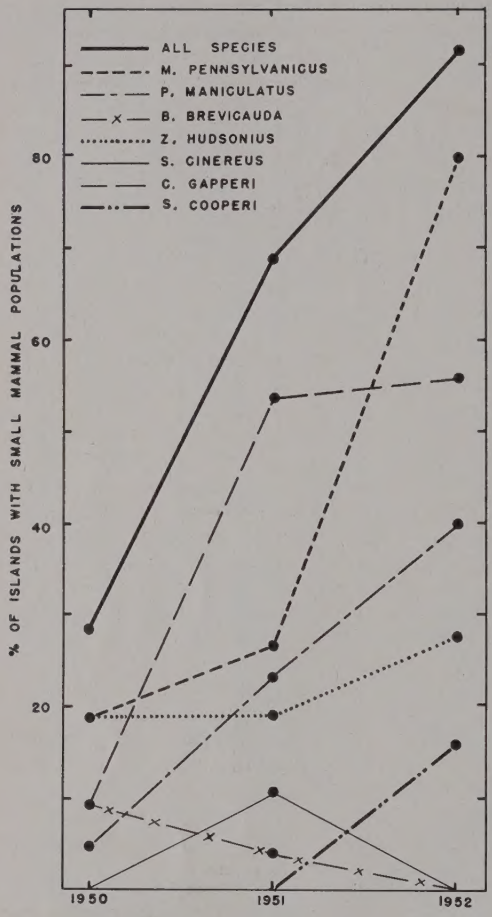

FIG. 2. Percentage of occupancy of the islands by the several species of small mammals studied from 1950 to 1952.

total occupancy to about 95 per cent in 1952. Only the jumping mouse of the hibernators was found on the islands. During the three years of the study very little difference was found in the proportion of the islands occupied by them.

Among the non-hibernators the cricetid rodents showed considerable variation but definite trends in the proportion of islands occupied while the shrews appeared to be entirely erratic in their distribution. The meadow mouse had the greatest variation in the proportion of the islands occupied. In 1950 they were found on 4 of the 21 islands trapped. There was some increase in 1951 but in 1952 21 of the 24 islands trapped were found to be occupied by this species. The red-backed mouse showed considerable increase in occupancy of islands during the study but unlike the meadow mouse its major increase came in 1951. The deer mouse was found on but one of the 21 islands trapped in 1950 but showed a steady increase so that in 1952 10 out of 24 islands were occupied by this species. The remaining species, the short-tailed shrew, the cinereous shrew and the lemming mouse, were not trapped on more than two or three islands each year. None of these were taken in all three years.

Along with the increase in the percentage of islands occupied there was an increase in the number of species found on individual islands (see Fig. 3) even though the average number of species per occupied island did not change appreciably. The average number of species per occupied island was 2.0, 1.9, and 2.3 for the three years respectively. Examination of Table II will show the changes found on individual islands. Island no. 3 was known to have one species in 1950 and four species in 1952, and island no. 20 was known to have 2, 4 and 5 species for the same period. Island no. 17 was the only island where a decrease was recorded. A single *Microtus* was recorded in 1950 and none since.

Live trapping was carried out on islands no. 3, 6, 15, and 23 with animals being tagged and released at the point of capture on islands 3 and 15.

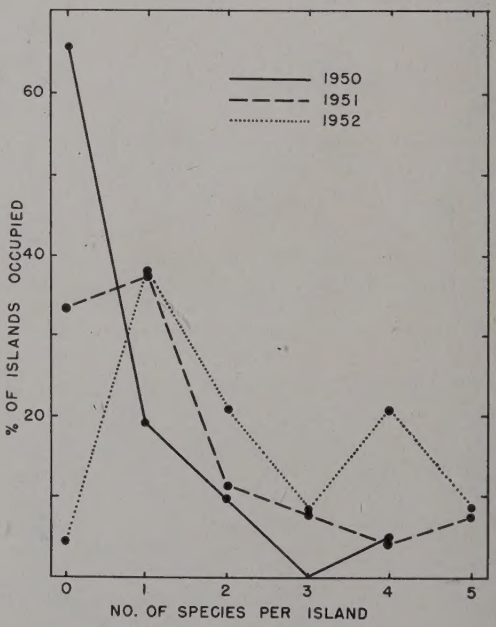

FIG. 3. The percentage of islands occupied by different numbers of species during the period of study.

Small mammals captured on the mainland were tagged and released on several islands (see Table III). Some 56 small mammals were also tagged in 1951 by Mr. Frenzel on island 12. In 1952 five of the tagged animals were retaken. Two adult female deer mice were found to have moved between islands 4 and 6 and 13 and 14, neither individual traveling more than 300 feet. One meadow mouse moved from island 12 to island 13, which is a distance of nearly one and one-half miles (see Fig. 1). The other two tag returns were from deer mice and were retaken on the same island where they were released after tagging.

TABLE III. *Live Trapping and Planting Data—1951.*

Island	Peromyscus maniculatus	Microtus pennsylvanicus	Clethrionomys gapperi
1.....	2	..	..
2.....	12	..	2
3.....	1*	..	2*
4.....	4	..	1
13.....	6	8	5
15.....	4*	..	..
16.....	..	2	..
17.....	..	..	2
18.....	5	..	..
19.....	3	..	..
22.....	..	2	..
23.....	2	..	..
26.....	..	..	2

*Released at point of capture.

Mr. Clifford Algren, resident forester for the Quetico-Superior Wilderness Research Center, informed us that he saw many tracks in the snow on the lake ice during the winter of 1951-52 but poor tracking conditions prevented him from following them for any distance.

On the basis of trapping and general observations it seemed evident that the small mammal populations were building up during the period of the study. The trapping data given in Table IV show that this was the case with the more common species. So few shrews were taken that no conclusions can be drawn for them. During the summer of 1950 one chipmunk was heard, but none seen; in 1951, the eastern chipmunk became fairly common and during the summer of 1952 both the eastern and least chipmunk were quite numerous. During the winter of 1951-52 there was considerable damage done to young pine trees through girdling by mice. This was not noted during the winters of 1949-50 or 1950-51. In the summer of 1952 mice were seen regularly throughout the area. During the previous two years mice were seldom seen. The buildup of population density on the islands appears to come a little later than on the mainland.

During the course of the study considerable difference was noted in the vulnerability of the several populations to trapping. Not only were there interspecific differences (see Fig. 4) but also differences among the various populations of the same species. The latter seemed to be correlated to the size of the islands from which they were taken (see Figs. 5, 6 and 7).

The deer mouse showed the greatest vulnerability to trapping. About 58 per cent, 67 per cent and 87 per cent of these animals taken were captured the first day of the three-day trapping period on the mainland, large islands and small islands respectively.

The red-backed mouse showed vulnerability similar to that of the deer mouse although it was not trapped quite so readily. This is shown by 50 per cent, 64 per cent and 75 per cent of the total

TABLE IV. *Relative abundance of small mammals as shown by trapping success.*

Year	Area	Trap days	Captures per 1000 trap days								
			Soricidae	Microtus pennsylvanicus	Peromyscus maniculatus	Clethrionomys gapperi	Synaptomys cooperi	Eutamias minimus	Tamias striatus	Zapus hudsonius	Totals
1950*	Island.....	1183	3.4	4.2	1.7	4.2	0	0	0	8.4	22.0
	Mainland.....	203	0	24.6	19.7	4.9	0	0	0	4.9	54.1
1951	Island.....	4258	3.1	4.5	22.3	20.7	0	0	0	2.1	52.1
	Mainland.....	246	16.3	16.3	16.3	36.6	0	0	0	0	81.3
1952	Island.....	4447	0	34.2	22.5	33.7	1.6	0	0	4.5	96.5
	Mainland.....	1524	0	42.0	22.3	15.1	1.3	1.9	3.9	1.3	86.6

*The figures given here for 1950 are undoubtedly relatively high as compared with those of 1951 and 1952 since the traps were left out but a single day at a place in 1950 and three days at a place in 1951 and 1952.

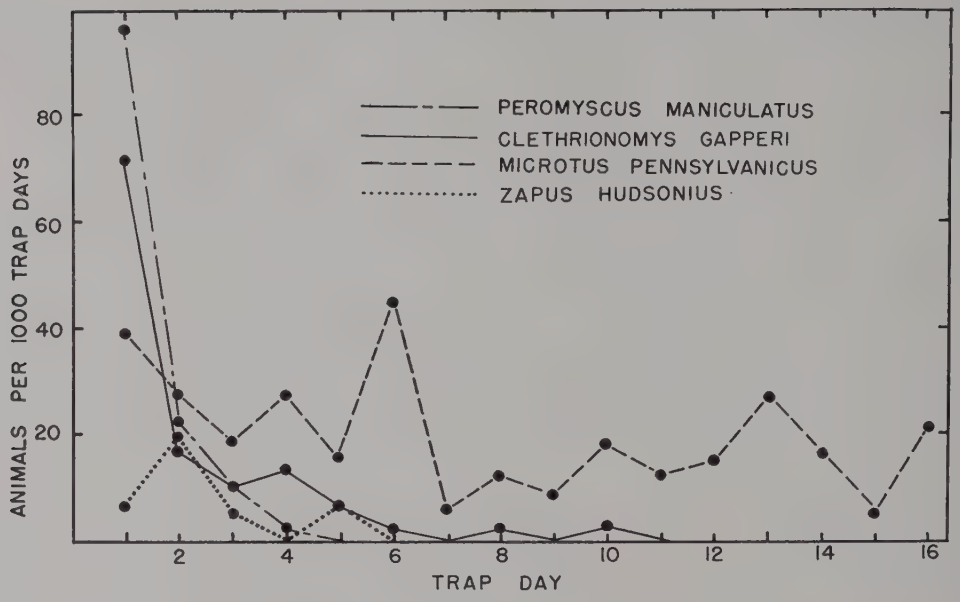

FIG. 4. Captures per thousand trap days to show r elative vulnerability to trapping among the four main species of small mammals on the islands.

catch being taken the first day on the three types of areas.

The meadow mouse is a more difficult species to work with, and trapping results show that it does not enter traps so readily as the deer or red-backed mice. On the islands the trends are similar to those found in the previous two species but the differences between the classes of islands and mainland are not as impressive. About 40, 54 and 46 per cent of the total captures were taken on the first day of trapping.

Four islands were also trapped for a considerable period of time (up to 16 days) in an attempt to remove all of the small mammals (see Fig. 4). In this attempt snap traps were set on a 15-foot grid. All of these islands had meadow, deer and red-backed mice. The last specimens taken of the first two species were caught on the fourth and tenth days of trapping while the meadow mice were still being taken at the end of the 16-day period.

The measurement of trap vulnerability is based on the assumption that each of the three days' trapping secures a similar proportion of the population present and that the higher the proportion of the total catch that is taken the first day, the more susceptible the population is to trapping. Islands of over nine acres in size were considered large and those below this in size were considered small. Since the trapping techniques varied somewhat with the size of the island the data may not be entirely comparable and it is difficult to evaluate the differences that may show up due to this.

These data indicate that a given mouse, on an island of the sizes studied, is more likely to be caught than if it occupied an area on the mainland. This suggests two possibilities: first, that the home range of the individual on an island is more restricted than if it were on the mainland and, secondly, that the daily travels of the mouse cover its home range more completely on an island than on the mainland. Further temporary ingress or egress may affect the results on the larger areas.

The trapping curves (Figs. 4, 5, 6 and 7) suggest that the deer mice are very readily taken if present. It seems doubtful that this species would be missed when trapping on the islands used in this study. Red-backed mice are somewhat less vulnerable to trapping than the deer mice but likewise should not be missed by trapping operations. The meadow mouse presents a different problem. It is relatively difficult to trap and it seems that small populations could be missed by the methods used. This is somewhat at variance with the work of Manville (1950), who felt that he handled all of the independent meadow mice on Little Rogg Island in Lake Michigan.

The other species were not taken in great enough

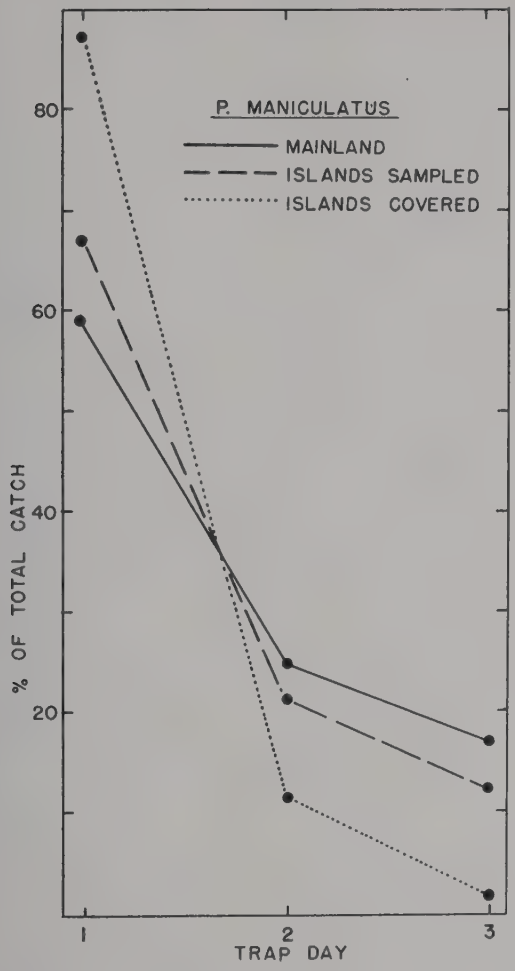

FIG. 5. Percentage of the total catch of *Peromyscus maniculatus* in relation to the day of capture showing relative vulnerability to trapping under different conditions.

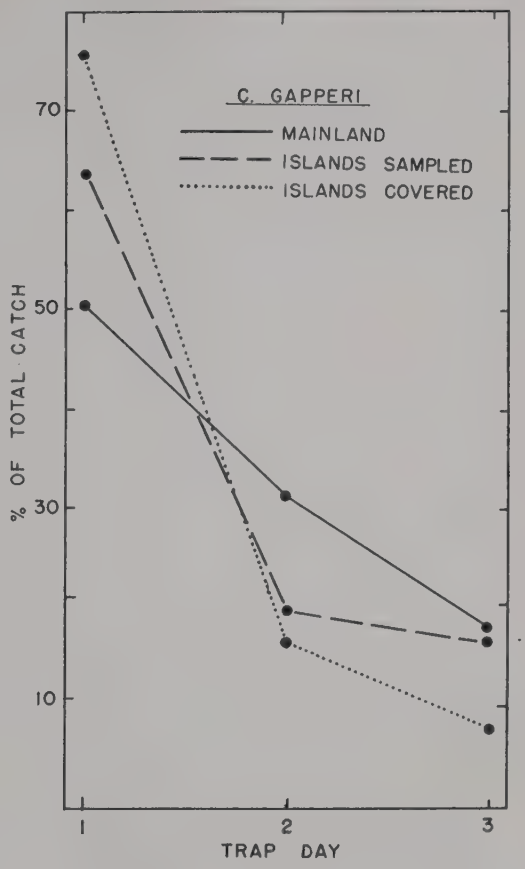

FIG. 6. Percentage of the total catch of *Clethrionomys gapperi* in relation to the day of capture showing relative vulnerability to trapping under different conditions.

numbers to warrant discussion. The erratic fluctuations shown by them may reflect normal sampling error for these small samples.

DISCUSSION

Direct observations on the isolation or lack of isolation of populations of small mammals on the several islands studied were not possible but the trapping data seem to shed considerable light on the situation. The jumping mouse was the only hibernator found on the islands. As it is active only during the warmer portions of the year the only apparent methods of colonizing the islands seem to be (1) swimming, (2) driftwood and (3) by hitching a ride in a boat or canoe. Since the islands that were most frequently visited by humans were inhabited at about the same rate as those in the more out-of-the-way places, it seems that the last method is of little importance. It also appears that swimming, except in a few cases where distances are short, could not be important with the jumping mouse. Transportation by driftwood was suggested as being very important by McCabe and Cowan (1945) and provides the most logical method of colonization in this area even though the drift would be on a much smaller scale. The jumping mouse frequents wet areas and it is reasonable that they would occasionally be caught on drift as it is washed from shore during periods of high water. The two chipmunks tend to frequent higher ground and they would thus have less chance by being transported by this method. It is probable that water serves as an effective barrier to the hibernating species and the

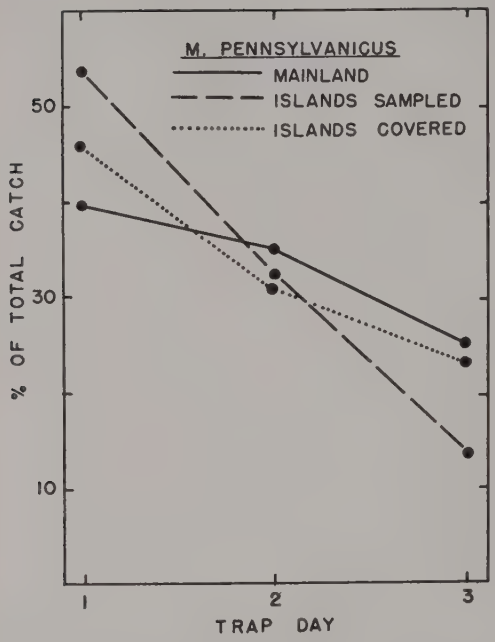

FIG. 7. Percentage of the total catch of *Microtus pennsylvanicus* in relation to the day of capture showing relative vulnerability to trapping under different conditions.

islands are but infrequently colonized by them.

The common species of non-hibernators, the meadow mouse, red-backed mouse, and deer mouse, apparently have considerably different relationships to the islands. During the summer these species should have about the same chances for water travel as the hibernators. Again, it is unlikely that they are capable of swimming any great distances, and the possibility of hitching a ride on a boat also seems remote. This is borne out by the fact that the deer mice, whose habits appear to make them best suited for this type of travel, were not found on island 12 which was a major camp site for canoeists. Driftwood again seems to offer the most plausible explanation for any summer colonization that may take place. That colonization is frequent and successful with this group is evident from the increase in the proportion of islands occupied in 1951 and 1952 as compared with 1950. Assuming that the trapping method used successfully ascertained the presence or absence of a species on an island, there were at least 39 cases of successful colonization by the non-hibernators. That mice may move from island to island is demonstrated by the movement of tagged animals. The observations on mouse tracks out on the ice and the lack of evidence for summer colonization indicates that colonization takes place primarily during the winter.

It is possible that there is a fairly constant proportion of the population that is on the move and that the rate of colonization of new habitat would be directly proportional to the density of the parent population. It seems more likely that while there may be some animals on the move at all times the proportion of transient animals is increased as higher population densities develop (Errington 1946). The population densities on the island are slower to build up than those on the mainland, suggesting that the density on the mainland must build up before there are enough animals on the move to colonize the islands.

In order to have islands to colonize, there must also be pressures towards the extirpation of the populations on these areas. During periods of low-density populations on the mainland the rate of colonization must drop below the rate of extirpation so that many of the islands lose their small mammal populations. Conversely, when the populations on the mainland are high, the rate of colonization is higher than the rate of extirpation and the proportion of islands with small mammal populations increases. It is also possible that the rate of extirpation as well as colonization changes considerably from year to year.

It was found that the smaller islands seldom had more than one or two species of small mammals present while the larger islands normally have four or five species (see Table III). Not only do the larger islands support more species per island than the small islands at any given time but they do not show the tendency to completely lose the population of the one or more species present. This indicates that the larger islands should be less dependent upon the mainland for periodic restocking than the small islands. The data presented show that the several populations vary greatly in degree of occupancy of the islands in different years. Also the density of any given species fluctuates considerably. While the data were not gathered over a long enough period of time to demonstrate the presence or absence of any cyclic behavior it does suggest that the several species may fluctuate independently of each other.

SUMMARY

During 1950, 1951 and 1952 studies on small mammals were carried on on the islands in Basswood Lake in Minnesota. The area was glaciated during the Pleistocene Epoch and has a poorly developed drainage system. The original dominant vegetation was made up primarily of conifers

but since logging operations and the burning and reburning that followed this logging, aspen and white birch have taken over the role as dominants.

Thirty-two islands and 5 mainland areas were chosen for the study. Three species of hibernators, *Eutamias minimus, Tamias striatus* and *Zapus hudsonias* were taken on the mainland with only the *Zapus* being found on the islands. All six of the non-hibernating species taken were found on the islands. These include *Microtus pennsylvanicus, Synaptomys cooperi, Clethrionomys gapperi, Peromyscus maniculatus, Blarina brevicauda* and *Sorex cinereus.*

The degree of occupancy changed from 4 out of 21 islands in 1950 to 21 of 24 islands in 1952. Along with this increase in the proportion of islands occupied there was an increase in the number of species found on most of the islands although the average number of species found on each occupied island did not change appreciably. This increase in islands occupied was correlated with an increase in the density of the mainland populations.

The water seemed to be an efficient barrier to travel during the summer but the ice of winter became a highway for dispersal of the various non-hibernating species in the winter.

Considerable difference was found in the vulnerability of the several species to trapping. The *Peromyscus* were readily caught. The *Clethrionomys* were not as easy to capture as the former but were still readily taken. The *Microtus,* however, posed a different problem. They were difficult to capture and on two islands of about 2.2 and 4 acres respectively we were not able to eliminate them after 16 days of trapping on a 15-foot grid.

The populations of small mammals fluctuate quite widely and the several populations appear to be somewhat independent of each other. The islands appeared to lag behind the mainland in the development of their populations.

References

Errington, P. L. 1946. Predation and vertebrate populations. Quart. Rev. Biol., **21**: 144-177, 221-245.

Manville, R. H. 1950. A comparison of trapping methods. Jour. Mamm., **31**: 377-383.

McCabe, T. T. and I. McT. Cowan. 1945. *Peromyscus maniculatus macrorhinus* and the problem of insularity. Trans. Royal Canadian Inst., **25**: 117-216.

Rosendahl, C. O. and **F. K. Butters.** 1928. Trees and shrubs of Minnesota. vii + 385 pp. (Ref. pp. 7-12). Univ. Minnesota Press, Minneapolis.

Thiel, G. A. 1947. The geology and underground waters of northeastern Minnesota. Minn. Geol. Survey Bull., **32**: xiii + 247 pp. (Ref. pp. 154-162).

U. S. Dept. of Agr. 1941. Climate and Man. U.S.D.A. Yearbook. 1-1248 pp. (Ref. pp. 925-934).

Zumberge, J. H. 1952. The lakes of Minnesota, their origin and classification. Minn. Geol. Survey Bull., 35. xiii + 99 pp. (Ref. pp. 1-9).

DISTANCE TO NEAREST NEIGHBOR AS A MEASURE OF SPATIAL RELATIONSHIPS IN POPULATIONS

Philip J. Clark and Francis C. Evans
Institute of Human Biology, University of Michigan, Ann Arbor, Michigan

Introduction

The pattern of distribution of a population of plants or of animals is a fundamental characteristic of that population, but it is a feature that is extremely difficult to describe in precise and meaningful terms. The distributions exhibited by populations of living organisms in their natural environments include an almost infinite variety of patterns. However, the lack of an adequate method of description has prevented the development of any system of pattern classification other than a most general one. The situation is further complicated by the fact that it has generally been considered necessary, for practical reasons, to use samples rather than entire populations as the source of distributional information, and this frequently introduces bias and inaccuracy into the estimates of population parameters. The whole problem of the measurement and description of patterns of distribution has recently been the subject of an excellent review by Goodall (1952) in reference to plant populations. It is evident from this review that many important concepts of phytosociology are based upon the assumption that the individuals of most plant populations are distributed at random. This assumption is no longer a tenable one, and it is probably even less applicable to animal populations. A number of methods of demonstrating the occurrence of non-random distribution are now available, but the degree of departure from random expectation is much more difficult to ascertain, and the significance of differences in the distribution pattern of two or more populations is therefore hard to evaluate. Im-

provement in the quantitative analysis of distribution is greatly to be desired and would surely facilitate the interpretation of dispersion patterns.

Gleason (1920) and Svedberg (1922) seem to have been the first ecologists to test natural distributions of organisms for conformity to random expectation, the former employing the binomial distribution and the latter making use of the Poisson series. Several measures have since been used to test the hypothesis of random dispersion. The data to which these measures have been applied are usually counts of individuals or records of presence or absence in sample plots or quadrats and are generally expressed in terms of frequency. Such data are strongly influenced by the size of quadrat used in their collection (Curtis and McIntosh 1950).

Recognition of the widespread existence of non-randomly distributed populations has led to the development of mathematical models based on various assumptions about the natural forces active in the formation of particular patterns. Some models (Ashby 1935) attribute primary importance to variations in environmental factors, others (Neyman 1939) to behavioral characteristics of the species concerned. Data from numerous sources have been fitted to these models, with varying degrees of success.

The distance from one individual to another provides a variable for the measurement of spacing that obviates the use of quadrats and therefore eliminates the effect of quadrat size. Viktorov (1947, *fide* Goodall 1952) measured the distance from a given plant to every other individual connected to it by a straight line not crossing another plant and used this information to estimate the variability of the distances. Cottam and Curtis (1949) attempted to ascertain the average distance between trees in a forested area by using "randomly selected" pairs of individuals. Dice (1952) seems to have been the first to use distance between nearest neighbors in measuring departure from randomness. Dice's procedure consists of measuring the distance from a randomly selected individual to its nearest neighbor in each of the six sextants of the circular area which surrounds the chosen "center of origin." The method is somewhat laborious, however, for it requires several measurements from each center of origin and makes use of third moment statistics in testing for the degree of departure from random expectation. One also experiences considerable difficulty in expressing the results of this measure in meaningful terms of spatial relations. Further study of the spacing problem has suggested the following measure, which requires but a single measurement from each center of origin and which we believe to be superior in its simplicity of computation and ease of interpretation. Use of the distance to nearest neighbor in the detection of non-randomness in spatial pattern has also recently been advocated by Skellam (1952), who has given a derivation of the probability distribution of this distance.

Lee R. Dice gave much advice and encouragement in the development of this measure. A letter from David G. Kendall, of Magdalen College, Oxford, offered a valuable suggestion for the derivation of a formula to express the mean expected distance between nearest neighbors in a random distribution of specified density. The measure of spacing described in this paper has been applied to the distributions of three species of grassland forbs charted by the junior author in collaboration with Stanley A. Cain and Fernando Segadas-Vianna, then associated with the Cranbrook Institute of Science, and also to a map of the trees of a woodlot prepared by Morrison Ismond, Bruce Hayward and Theodore Herman. Raymond H. Brand carried out many of the measurements and much of the statistical computation. To all of these sources of information and assistance we are very grateful. Both authors are jointly responsible for the ideas of this paper and have shared in the preparation of the manuscript. The senior author is primarily responsible for the mathematical derivations and statistical treatments.

The Measure

For the purposes of simplification, this measure of spacing is explained here in terms of two-dimensional space, *i.e.*, with reference to populations on plane surfaces. With suitable modification, however, it is equally applicable to populations distributed along a line or dispersed throughout a volume. A generalization of the measure for use with k dimensions has been worked out and will be published later.

The measure of spacing which we propose is a measure of the manner and degree to which the distribution of individuals in a population on a given area departs from that of a random distribution. Some clarification of what is meant by a "random distribution" is therefore desirable. In a random distribution of a set of points on a given area, it is assumed that any point has had the same chance of occurring on any sub-area as any other point, that any sub-area of specified size has had the same chance of receiving a point as any other sub-area of that size, and that the placement of each point has not been influenced by that of any other point. Thus, randomness as here employed is a spatial concept, intimately dependent upon the boundaries of the space chosen by the investigator. A set of points may be random with respect to a

specified area but decidedly non-random with respect to a larger space which includes the specified area. For meaningful results, therefore, the areas selected for investigation should be chosen with care.

The distance from an individual to its nearest neighbor, irrespective of direction, provides the basis for this measure of spacing. A series of such distances is measured in a given population, using all of the individuals present or a randomly selected sample, and the value of the mean distance to nearest neighbor is obtained for this set of observations. The mean distance to nearest neighbor that would be expected if the individuals of that population were randomly distributed is also calculated. The ratio of the observed mean distance to the expected mean distance serves as the measure of departure from randomness. The ratios that have been calculated for two or more populations can be directly compared with one another, as a measure of their relative departure from random expectation. Significance tests of the difference between ratios can be made without great difficulty, and the results of comparison can be expressed in terms that are readily visualized. To facilitate presentation, the derivation of some of the formulas used in this paper are included in an Appendix rather than in the body of the text. A list of the symbols and definitions of concepts employed herein is given in Table I.

TABLE I. *A list of the symbols and definitions of concepts employed in a measure of spacing based on the mean distance between nearest neighbors*

N	the number of measurements of distance taken in the observed population or sample. When a single sector is employed, N is also equal to the number of individuals used as centers of measurement.
r	the distance in any specified units from a given individual to its nearest neighbor.
ρ	the density of the observed distribution expressed as the number of individuals per unit of area. (The unit of measurement used in the calculation of rho must be the same as that used in measuring r.)*
Σr	the summation of the measurements of distance to nearest neighbor.
Σr^2	the summation of the squares of the measurements of distance.
$\bar{r}_A = \frac{\Sigma r}{N}$	the mean of the series of distances to nearest neighbor.
$\bar{r}_E = \frac{1}{2\sqrt{\rho}}$	the mean distance to nearest neighbor expected in an infinitely large random distribution of density rho.
$R = \frac{\bar{r}_A}{\bar{r}_E}$	the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbor.
$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}}$	the standard variate of the normal curve.
$\sigma_{\bar{r}_E} = \frac{0.26136}{\sqrt{N\rho}}$	the standard error of the mean distance to nearest neighbor in a randomly distributed population of density rho.
F	the ratio of between-group variance to within-group variance in a test of significance of the differences between two or more populations.
p	the number of populations being compared.
k	the number of sectors in a circle of infinite radius surrounding the individual from which measurements of distance are taken.

*Computation of rho on the basis of N - 1 rather than N is theoretically proper, but with large samples the difference in results is negligible.

If, in a population of N individuals having a specified density ρ, the distance r from each individual to its nearest neighbor is measured, the mean observed distance may be represented as $\bar{r}_A = \frac{\Sigma r}{N}$. The mean distance which would be expected if this population were distributed at random, $\bar{r}_E$, can be shown to have a value equal to $\frac{1}{2\sqrt{\rho}}$ (see Appendix). The ratio $R = \frac{\bar{r}_A}{\bar{r}_E}$ can then be used as a measure of the degree to which the observed distribution approaches or departs from random expectation. In a random distribution, $R = 1$. Under conditions of maximum aggregation, $R = 0$, since all of the individuals occupy the same locus and the distance to nearest neighbor is therefore 0. Under conditions of maximum spacing, individuals will be distributed in an even, hexagonal pattern, and every individual (except those at the periphery of the population) will be equidistant from six other individuals. In such a distribution, the mean distance to nearest neighbor will be maximized and will have the value $\frac{1.0746}{\sqrt{\rho}}$ (see Appendix). When this is the case, $R = 2.1491$. Thus, R has a limited range, with values indicative of perfectly uniform, random, and completely aggregated patterns of distribution. In any given distribution, the mean observed distance to nearest neighbor is R times as great as would be expected in a random distribution of the same density. Thus, an R value of 0.5 would indicate that nearest neighbors are, on the average, half as far apart as expected under conditions of randomness. This measure can therefore be readily interpreted in simple terms. Since it is also easily computed, it should be of practical use in describing spatial relations.

TESTS OF SIGNIFICANCE

The usefulness of any measure of spacing will be increased if its reliability can be ascertained. If the value of R indicates that a given population is not randomly distributed, the significance of the departure of $\bar{r}_A$ from $\bar{r}_E$ can be tested by the normal curve. The formula used in this test of significance is

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}}$$

where c is the standard variate of the normal curve (Mather 1947) and $\sigma_{\bar{r}_E}$ is the standard error of the mean distance to nearest neighbor in a randomly distributed population of the same density as that of the observed population. The value of $\sigma_{\bar{r}_E}$ for a population of density ρ is $\frac{0.26136}{\sqrt{N\rho}}$, where N is the number of measurements of distance made (see Appendix). The c values 1.96 and 2.58 represent respectively the 5 per cent and the 1 per cent levels of significance (for a two-tailed test); for other values one may consult a table of the normal distribution.[1]

When two populations are being compared, it may not be sufficient merely to ascertain whether each of them departs significantly from randomness. One may also want to know whether the populations differ significantly from one another with respect to the direction and magnitude of their departures from random expectation. The significance of the difference in the values of R for two populations can be tested by the Student-Fisher t distribution, or by the F distribution. We have employed the latter method because it can be used with more than two populations (see Appendix for analysis of variance).

The tests of significance proposed above are based on the difference between $\bar{r}_A$ and $\bar{r}_E$. It is theoretically possible, however, for a non-randomly distributed population to exist in which $\bar{r}_A$ and $\bar{r}_E$ are equal. The distribution of such a population cannot be shown to be non-random by these tests. In this case, departure from randomness may be ascertained by comparing the frequency distributions of observed and expected distances to nearest neighbor by means of a χ^2 test (for procedure, see Cochran 1952). The majority of investigations of natural populations, however, will not require so sensitive a test.

Application of the Measure to Actual Data

The measure described above has been tested experimentally by applying it to a synthetically constructed random distribution, to the distributions of three species of grassland plants whose patterns exhibit various degrees of aggregation, and to the distribution of trees participating in the canopy of a woodlot, where competition for light might be expected to bring about a comparatively uniform spacing. The results of these analyses are shown in Table II.

[1] When N is small, somewhat greater accuracy in this test of significance may be obtained by use of the Pearson type III distribution than by use of the normal curve. It can be shown that the skewness of the distances to nearest neighbor in a randomly dispersed set of points on a plane surface is $\alpha_3 = .631$. The probability of a given difference between $\bar{r}_A$ and $\bar{r}_E$ should therefore be found, with the type III distribution, under $\alpha_3 = \frac{.631}{\sqrt{N}}$. When N is large, say over 100, the difference in results is negligible.

Table II. *Comparison of certain statistics obtained in the application of the measure of spacing to various distributions. Measurements for the synthetic random distribution are in units of millimeters and square millimeters, those for the other distributions in units of feet and square feet*

Statistic	Synthetic random	*Solidago*	*Liatris*	*Lespedeza*	Forest trees
Size of area	25,781	23,936	23,936	23,936	69,696
N	116	89	197	184	174
ρ	.0044944	.00371825	.00823028	.00768717	.00249656
$\sqrt{\rho}$	.0670779	.0609774	.0907209	.0876765	.0499656
Σr	833.12	530.24	601.57	512.60	1979.99
Σr^2	7909.6616	4751.5652	4587.6121	3385.5290	30382.6942
$\bar{r}_A$	7.1821	5.9578	3.0537	2.7859	11.3793
$\bar{r}_E$	7.4540	8.1998	5.5114	5.7028	10.0069
R	0.9635	0.7266	0.5541	0.4885	1.1371
$\sigma_{\bar{r}_E}$	0.3618	0.4543	0.2053	0.2198	0.3965
c	0.75	4.93	11.97	13.27	3.46
Probability of a greater difference between $\bar{r}_E$ and $\bar{r}_A$	.453254	.000002	.000002	.000002	.000540

A synthetic random distribution

An artificial distribution was constructed on cross-section paper of 20 lines per inch by random placement of 116 points on a rectangle of 203 x 116 mm. The distance to the nearest neighbor was measured for each point, and the mean observed distance to nearest neighbor proved to be 7.1821 mm. while the mean expected distance was calculated to be 7.4540 (Table II). For this synthetic distribution, R = 0.96, not far from the 1.00 expected of a perfectly random distribution. A test of the significance of the difference between observed and expected mean distances gave a c value of 0.75, indicating that greater departure from expectation might occur 45 per cent of the time purely by chance. The synthetic model was thus shown to be a satisfactory representation of random dispersion.

Distributions of grassland plants

The locations of all individuals of *Lespedeza capitata* Michx., *Liatris aspera* Michx., and *Solidago rigida* L. occurring on several acres of an abandoned field on the University of Michigan's Edwin S. George Reserve were recently mapped by Cain and Evans (1952). Inspection of the

map and quantitative studies of the distributions by Thomson (1952) and Dice (1952) indicated that *Lespedeza* was the most strongly aggregated of the three species, whereas *Solidago* was the least aggregated. The measure of spacing described above has been applied to the distribution patterns of these plans on a portion of the map having field dimensions of 136 x 176 feet. The results of analysis are shown in Table II. For *Lespedeza,* $R = 0.49$, for *Liatris,* $R = 0.55$, and for *Solidago,* $R = 0.73$, thus confirming the relative degrees of aggregation shown by previous studies. None of these R values is close to 1, and in each case the probability of obtaining, in a random distribution of the same density, a c value as large as that observed is less than .000002. All three populations clearly depart from random expectation with a high degree of significance, so far as the distance to nearest neighbor is concerned. An analysis of variance was made for an over-all comparison of the three species and yielded an F value of 4.57, significant at the 5 per cent level, indicating differences in the degree of aggregation. Analysis of individual differences, by the methods of Tukey (1949), then showed that *Solidago* differed from both *Liatris* and *Lespedeza,* but the latter two populations were not shown to differ from each other.

A distribution of forest trees

The measure has also been used to evaluate the spacing between individual trees which formed the canopy of an oak-hickory woodlot on the North Campus of the University of Michigan. The distribution pattern of these trees was not readily discernible, although it was suspected of being more uniform than random. Analysis of the trees which occurred on a square plot of this woodlot measuring 264 feet on a side gave the results indicated in Table II. For this distribution, $R = 1.14$, indicating a departure from random expectation in the direction of uniformity. This difference was shown to be highly significant by the c test.

Application of the Measure to Large Populations

This measure of spacing requires that the true density of the population under investigation be known. Such knowledge permits the calculation of the exact values of the mean expected distance to nearest neighbor and of its standard error. If an estimate of mean density is substituted for its true value, the rigor of the proposed tests of significance will be lost. We recommend, therefore, that the measure be applied to populations which are small enough to permit ascertainment of the true density. This will involve a complete count or census of the population.

If it is considered impractical to measure the distance to nearest neighbor for all of the individuals in the area selected for study, an estimate of the mean distance can be obtained from a random sample and can be used in the formulas already presented. To obtain a truly random sample of n individuals, it is necessary that every possible combination of n individuals have an equal chance of being drawn. This requires that every individual be identified, *i.e.,* marked in some manner, and that n of these marked individuals be drawn at random. In some situations, this may be impractical and the investigator may wish to obtain his measurements of distance to nearest neighbor from randomly selected quadrats. Some rigor will be lost by this procedure, but the saving in time may be considerable. The method of selecting quadrats at random will differ according to circumstances. Time and labor will be saved if the locations of all quadrats to be examined are established prior to collection of data, for the examination of quadrats can then proceed according to location rather than order of draw. The measurements of distance to nearest neighbor obtained in the series of quadrats should be pooled to provide an estimate of $\bar{r}_A$. This estimate may be used in the estimate of R and in the tests of significance given above but is less satisfactory than an estimate based upon a truly random sample.

The problem of the size of sample needed for a satisfactory estimate is discussed in many statistical textbooks and additional space need hardly be devoted to it here. Briefly, however, the size of sample (*i.e.,* number of individuals) required depends upon the degree of accuracy with which the investigator will be satisfied and upon the variability in the distance to nearest neighbor. The more variable the distance, the larger the size of the sample needed to provide a specified degree of accuracy. In general, it may be said that the less uniform the spacing of the individuals in the population, the greater the variability in distance to nearest neighbor will be and the larger the sample required. In any given case, the number of quadrats needed to secure a sufficient sample will depend upon the size of quadrat used. If many small quadrats are used, the sample will more closely approximate a random sample as defined above, and will therefore be more satisfactory, than if a few large quadrats are employed.

Problems of Procedure

When measurements are being taken, one may find that the nearest neighbor of a given individual lies outside of the specified area. Such distances should be measured and included in the computations. However, no individual lying outside the

specified area should be used as a center of measurement.

It may also happen that two individuals selected as centers of measurement are closer to one another than to any other individuals. In this case, the same distance will be measured twice. Such double distances introduce no bias and both measurements should be used in the calculations.

The derivation of the mean expected distance between nearest neighbors in a randomly distributed population of specified density is based on the assumption that the area occupied by the population is infinite. In practice, however, we apply the measure to finite populations occupying definite areas. The presence of a boundary beyond which measurements cannot be made will tend to make the value of $\bar{r}_A$ greater than would be obtained if an infinite area were involved. For this reason it will be desirable, whenever possible, to select an area for investigation that lies well within the total area covered by the entire population.

In the foregoing description of this measure of spacing, the individual components of a population have been treated as dimensionless points, whereas in reality they will occupy definite areas. In many situations, the area occupied by an individual is so small in relation to the total area under examination that the individual can legitimately be treated as a point. However, if the individual occupies an area of some size it can no longer be treated as a point, and its spatial requirements become important in determining its relationship to other individuals. In such cases, this measure of spacing is applicable only to the centers of individuals, and measurements of distance should be taken accordingly. It is possible for individuals to be as closely spaced as their size permits and at the same time to have their centers distributed more uniformly than random. Consequently, R values greater than unity may sometimes result from the spatial requirements of the individuals alone.

Extension of the Method

A description of distribution pattern solely in terms of the distance to nearest neighbor is not entirely complete, for it disregards all of the other spatial relations which exist in a population. The measure as described above may therefore not distinguish between certain types of distribution patterns. For example, a population whose individuals are congregated in one spot will not be distinguished from a population consisting of scattered pairs of individuals, such as conjugating *Paramecium,* for in each case the distance to nearest neighbor will be 0. In such situations, the measure can be extended to make use of additional space relations.

Consider each individual selected as a center of measurement to be surrounded by a circle of infinite radius, which can be divided into equal sectors. The distance from the individual at the center to the nearest individual in each of the sectors can then be measured. These distances become the basis of calculations. In this case, the formulas (1) for the expected mean distance to nearest neighbor in a randomly distributed population of density ρ and (2) for its standard error are respectively $\bar{r}_E = \frac{\sqrt{k}}{2\sqrt{\rho}}$ and $\sigma_{\bar{r}_E} = \frac{0.26136\sqrt{k}}{\sqrt{N\rho}}$ where N is the number of measurements and k is the number of sectors about each individual used as a center of measurement. The ratio of the observed mean distance to nearest neighbor to the mean distance expected if the population were randomly distributed will again indicate deviation from randomness whenever its value is greater or less than 1. For completely aggregated populations, its value is, of course, 0. The value indicative of perfectly even, hexagonal spacing depends upon k and is equal to $\frac{2.1491}{\sqrt{k}}$ when k is not greater than 6.

It should be pointed out that an increase in the number of sectors may not always result in greater knowledge about the population under investigation. For example, the *Liatris* and *Lespedeza* populations previously described were re-examined using 2, 3 and 6 sectors. In no case was a significant F value obtained, and the conclusions as to spacing were identical with those based on a single sector. The number of sectors to be used in any given situation, therefore, will depend upon the nature of the distribution patterns involved. Caution should be observed when increasing the number of sectors, for the assumptions underlying the derivations of $\bar{r}_E$ and $\sigma_{\bar{r}_E}$ preclude the existence of empty sectors. We believe that the use of a single sector, *i.e.,* the entire circular area surrounding an individual chosen as a center of measurement, will be sufficient for the description and comparison of spatial relations in most natural populations.

An alternative to the use of more than one sector might be developed by employing successively the second, third, etc. nearest neighbors. The formulas for such a procedure would, however, be more complex than those used in this paper and we have not attempted to explore this possibility.

Summary

To obtain a measure of the spacing of individuals in a population of known density, the distance, r, from each individual to its nearest neighbor may be measured and the mean value of r, here designated $\bar{r}_A$, computed. The mean value of r which would obtain in an infinitely large random distribution of density ρ is found by the formula $\bar{r}_E = \frac{1}{2\sqrt{\rho}}$. The ratio $R = \frac{\bar{r}_A}{\bar{r}_E}$ of observed to expected mean distance provides a measure of the degree to which the distribution pattern of the observed population deviates from random expectation. This ratio is less than, equal to, or greater than 1 according to whether the distribution pattern of the individuals in the population is more aggregated, the same as, or more uniform than would be expected in an infinitely large random distribution of the same density. R ranges in value from 0 for a distribution with maximum aggregation to 2.1491 for a distribution which is as evenly and widely spaced as possible. The significance of departure from random expectation on the part of a given population may be tested by the normal variate

$$c = \frac{\bar{r}_E - \bar{r}_A}{\sigma_{\bar{r}_E}}$$

where $\sigma_{\bar{r}_E}$, the standard error of $\bar{r}_E$, is $\frac{0.26136}{\sqrt{N\rho}}$. The significance of the differences between values of R from various populations may be tested by a one-way analysis of variance.

To demonstrate the simplicity and ease of interpretation of this measure, it has been applied to a synthetically constructed random distribution, to the distribution of three species of grassland plants whose patterns showed various degrees of aggregation, and to the distribution of trees in an oak-hickory woodlot where the pattern was suspected of being more uniform than random. For the synthetic distribution R = 0.96, a non-significant deviation from unity. The three grassland populations yielded the following R values: 0.73 for *Solidago,* 0.55 for *Liatris,* and 0.49 for *Lespedeza,* all of which are significant departures from randomness in the direction of aggregated spacing. For the trees of the woodlot, R = 1.14, a significant deviation from randomness in the direction of uniform spacing.

This measure requires a knowledge of the true density of the population. If this is known, it can be applied to populations in which it is considered impractical to measure the distance to nearest neighbor for all of the individuals. In such cases an estimate of the mean distance to nearest neighbor may be substituted for its true value. This estimate will give more satisfactory results if it is based upon a truly random sample of individuals but it can be obtained from randomly selected quadrats. The size of sample and the number and size of quadrats required are discussed briefly.

Since this measure involves only the relationship between a given individual and its nearest neighbor, the majority of spatial relations in the population are ignored. An extension of the method may be achieved by constructing a circle of infinite radius about each individual from which distances are to be measured, dividing this circle into equal sectors, and measuring the distance from the individual at the center to the nearest neighbor in each of the sectors. The occurrence of empty sectors should be avoided. It is believed that for most purposes a single sector, *i.e.,* the entire circle surrounding the individual chosen as a center of measurement, will be adequate.

An appendix to the paper gives the derivation of certain formulas employed in the development of the measure.

Appendix

Derivation of formulas for $\bar{r}_E$ *and* $\sigma_{\bar{r}_E}$

The formula for the mean distance to nearest neighbor expected in a randomly dispersed population of specified density seems first to have been derived by Hertz (1909). This paper is virtually unknown to biologists and was brought to our attention by Dr. F. D. Miller, Department of Astronomy, University of Michigan, after the senior author had independently obtained the derivations given below. These are presented here because of the inaccessibility of Hertz's paper and because they are considerably simpler than those given by Hertz.

For a random distribution of points in two dimensions the probability that a randomly chosen area of specified size will contain exactly x points is, by Poisson's exponential function, $\frac{m^x e^{-m}}{x!}$, where m is the mean number of points per area. Let the specified area be a sector of a circle of radius r, formed by dividing the circle into k equal sectors. If ρ is the mean density of the distribution, then $m = \rho k^{-1} r^2$ is the mean number of points per area. In this case

$$\frac{(\rho\pi k^{-1}r^2)^x \, e^{-\rho\pi k^{-1}r^2}}{x!}$$

is the probability of finding exactly x points in an arbitrary area of $\pi k^{-1} r^2$ units. Consequently, $e^{-\rho\pi k^{-1}r^2}$ is the probability that a randomly chosen area of $\pi k^{-1} r^2$ units will contain no points. If our area is a sector of a circle about a randomly

chosen point, the probability that the sector will contain no other point within a distance r of the chosen point is also $e^{-\rho\pi k^{-1}r^2}$. Considered as a function of r, this is the proportion of distances to nearest neighbor (within sectors) $\geq r$. Consequently $1 - e^{-\rho\pi k^{-1}r^2}$ is the proportion of distances to nearest neighbor $\leq r$. Differentiating the last expression with respect to r we obtain $2\rho\pi k^{-1}re^{-\rho\pi k^{-1}r^2}dr$ as the probability distribution of r. The mean of r, called $\bar{r}_E$, can be obtained by multiplying the above expression by r and integrating over the interval from 0 to ∞. Thus $\bar{r}_E = \int_0^\infty 2\rho\pi k^{-1}r^2e^{-\rho\pi k^{-1}r^2}dr$, which can be shown to be $\frac{\sqrt{k}}{2\sqrt{\rho}}$.

The second moment of r, $E(r^2)$, is obtained by multiplying the probability distribution function of r by r^2 and integrating over the interval from 0 to ∞. Thus

$$E(r^2) = \int_0^\infty 2\rho\pi k^{-1}r^3e^{-\rho\pi k^{-1}r^2}\,dr.$$

This integral has the value $\frac{k}{\rho\pi}$. The variance of r is $E(r^2) - (\bar{r}_E)^2$, which proves to be $\frac{(4-\pi)k}{4\pi\rho}$. The standard error of $\bar{r}_E$, $\sigma_{\bar{r}_E}$, is thus

$$\sqrt{\frac{(4-\pi)k}{4\pi\rho N}} = \frac{0.26136\sqrt{k}}{\sqrt{N\rho}},$$

where N is the number of measurements made.

The upper limit of $\frac{\bar{r}_A}{\bar{r}_E}$

The mean distance between nearest neighbors is maximized in a hexagonal distribution, where each point has 6 equidistant nearest neighbors. Let r_u denote the constant distance between nearest neighbors in this distribution. In such a uniform distribution each point can be shown to occupy an area of $\frac{r_u^2 3^{1/2}}{2}$. The density, ρ, of the population is thus $\rho = \frac{2}{r_u^2 3^{1/2}}$. Solving for r_u we obtain $r_u = \frac{2^{1/2}}{3^{1/4}\rho^{1/2}}$. Since r_u is the greatest possible value of $\bar{r}_A$, the maximum value of the ratio $R = \frac{\bar{r}_A}{\bar{r}_E}$ is $\frac{r_u}{\bar{r}_E}$, or $\frac{2^{1/2}}{3^{1/4}k^{1/2}}$, which is approximately equal to $\frac{2.1491}{\sqrt{k}}$.

The application of the analysis of variance to the ratio R

In applying the analysis of variance, we desire to test for differences in R rather than $\bar{r}_A$. Since

$$R = \frac{\bar{r}_A}{\bar{r}_E} = 2\sqrt{\rho}\ \bar{r}_A$$

it is necessary to multiply each value of r by the square root of the density of the population to which it belongs. Such a transformation is most readily effected by multiplying each Σr by its corresponding $\sqrt{\rho}$ and each Σr^2 by its ρ. If p populations are being compared the following computational scheme may be used:

$$a = \rho_1\Sigma r_1^2 + \rho_2\Sigma r_2^2 + \ldots + \rho_p\Sigma r_p^2$$

$$b = \frac{(\sqrt{\rho_1}\Sigma r_1 + \sqrt{\rho_2}\Sigma r_2 + \ldots + \sqrt{\rho_p}\Sigma r_p)^2}{N_1 + N_2 + \ldots + N_p}$$

$$c = \frac{\rho_1(\Sigma r_1)^2}{N_1} + \frac{\rho_2(\Sigma r_2)^2}{N_2} + \ldots + \frac{\rho_p(\Sigma r_p)^2}{N_p}$$

where the subscripts 1, 2, . . . , p which follow ρ, r, and N represent the populations to which these data pertain. The variance ratio, F, for testing the significance of the difference in the values of R for the p populations is

$$F = \frac{(c-b)\,(N_1 + N_2 + \ldots + N_p - p)}{(a-c)\,(p-1)},$$

there being $p - 1$ and $N_1 + N_2 + \ldots + N_p - p$ degrees of freedom for the between-group and within-group variances respectively. If a significant F is obtained from this over-all analysis, we know that not all of the populations are alike in their degrees of clumping. The problem of ascertaining which populations differ from each other, however, is more complicated and will not be discussed here. Tukey (1949) has suggested ways of dealing with this problem.

References

Ashby, E. 1935. The quantitative analysis of vegetation. Ann. Bot. **49**: 779-802.

Cain, S. A., and F. C. Evans. 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich. **52**: 1-11.

Cochran, W. D. 1952. The χ^2 test of goodness of fit. Ann. Math. Statist. **23**: 315-345.

Cottam, G., and J. T. Curtis. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology **30**: 101-104.

Curtis, J. T., and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology **31**: 434-455.

Dice, L. R. 1952. Measure of the spacing between individuals within a population. Contrib. Lab. Vert. Biol. Univ. Mich. **55**: 1-23.

Gleason, H. A. 1920. Some applications of the quadrat method. Bull. Torrey Bot. Club **47**: 21-33.

Goodall, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. **27**: 194-245.

Hertz, P. 1909. Über den geigenseitigen durchschnittlichen Abstand von Punkten, die mit bekannter mittlerer Dichte im Raume angeordnet sind. Mathematische Annalen **67**: 387-398.

Mather, K. 1947. Statistical analysis in biology. Interscience Publishers, Inc., New York.

Neyman, J. 1939. On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. Math. Statist. **10**: 35-37.

Skellam, J. G. 1952. Studies in statistical ecology. I. Spatial pattern. Biometrika **39**: 346-362.

Svedberg, T. 1922. Ett bidrag till de statistiska metodernas användning inom växtbiologien. Svensk Bot. Tidskr. **16**: 1-8.

Thomson, G. W. 1952. Measures of plant aggregation based on contagious distributions. Contrib. Lab. Vert. Biol. Univ. Mich. **53**: 1-16.

Tukey, J. W. 1949. Comparing individual means in the analysis of variance. Biometrics **5**: 99-114.

Viktorov, S. V. 1947. A study of the distribution and dispersion of plants by aerial photographs. (in Russian) Bull. Soc. Nat. Moscou (sect. biol.), N.S. **52** (4): 71-78.

ECOLOGY OF SPECIES OF *MEGACHILE* LATREILLE IN THE MIXED PRAIRIE REGION OF SOUTHERN ALBERTA WITH SPECIAL REFERENCE TO POLLINATION OF ALFALFA[1]

G. A. Hobbs and C. E. Lilly[2]
Field Crop Insect Section, Science Service Laboratory, Lethbridge, Alberta, Canada

Introduction

In the semi-arid regions of western North America, bees of the genera *Megachile* Latr., *Bombus* Latr., and *Nomia* Latr. are considered the most important native bee pollinators of alfalfa (Tysdal 1940). In Utah, Bohart (1951) and Carlson *et al.* (1950) consider *Nomia melandri* Ckll. the most important in areas where it is prevalent. Species of *Nomia* are not found in southern Alberta. Sladen (1918), Gray (1925), and Salt (1940) gave some credit to bumble bees as pollinators of alfalfa in southern Alberta.

In 1950 Hobbs (1950) observed only one bumble bee tripping alfalfa, this record having been made prior to August 5. In 1951, 11 queens and workers of *Bombus nevadensis* Cress., *B. rufocinctus* Cress., *B. borealis* Kby., *B. occidentalis* Greene, and *B. huntii* Greene were taken on alfalfa but none were recorded before August 5. In 1952, 21 members of these species and *B. fervidus* (F.) were captured on alfalfa before August 15. (Experiments on pollination of alfalfa by honey bees indicated that the seed produced by flowers tripped after August 5 in 1950 and 1951, and after August 15, 1952, was destroyed by frost before it had time to mature.) Hence, only a few bumble bees were seen to trip alfalfa flowers, and still fewer did this at a time when tripping would have resulted in the production of mature seed. In 1951 and 1952 many workers of the common species *B. nevadensis, B. rufocinctus, B. fervidus,* and *B. huntii* were found to be gathering pollen from sweet clover that was growing near alfalfa. It is realized that certain species of bumble bees may be an important factor in certain isolated, mixed prairie areas where they are abundant and/or where competing plants, especially sweet clover, are few.

Osmia texana Cress. and *Anthophora occidentalis* Cress. have been found nesting gregariously in large colonies in cutbanks near alfalfa seed fields. Neither species has been seen to gather pollen or nectar from alfalfa by the writers.

Alfalfa is grown for seed in two ecological areas in Western Canada. Most of the seed is now produced in that area, referred to by Coupland (1950) as aspen "parkland" ecotone, which lies between mixed prairie and boreal forest and is associated with fescue grassland. The mixed prairie (*Stipa-Bouteloua* association), which is also an important alfalfa seed-growing area, is clearly defined by Coupland (1950). The borders of both fescue grassland and aspen parkland cannot be as clearly defined because they are associated with each other to some extent. Aspen poplar, *Populus tremuloides* Michx., is the principal, and often the only, tree species in the groves, or "bluffs," of the aspen parkland. The grassland between the groves is characterized by fescue, *Festuca scabrella* Torr. (This description was furnished by Dr. W. G. Dore, Senior Botanist, Botany and Plant Pathology Division, Ottawa, Canada.)

Most of the alfalfa grown for seed is grown on cleared land formerly covered with deciduous

[1] Contribution No. 3067, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada. Part of a thesis submitted by the senior author for the degree of Doctor of Philosophy, Oregon State College, 1952.

[2] Associate Entomologist and Assistant Entomologist.

bush. At present a large portion of the alfalfa seed produced in Alberta is grown north of latitude N 55° (Fig. 1). Commercial production has been extended to latitude 58° 30′. As the area designated as fescue grassland may be either prairie or parkland, distribution records from this ecological area give no clue as to a species' preferred habitat. However, the distribution of a species on mixed prairie and/or aspen parkland does indicate the preferred nesting habitat.

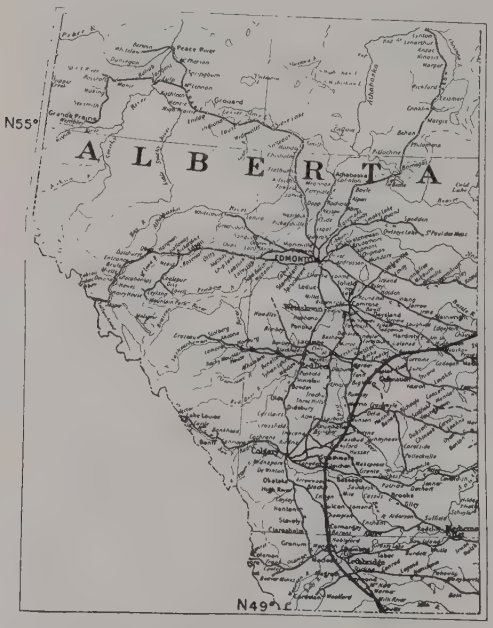

FIG. 1. Map of Alberta to N 56° 15′ showing the extent of mixed prairie east of bold line.

In the aspen parkland region alfalfa is grown on dry land, whereas in the mixed prairie it is grown on irrigated land. Although the problem is fundamentally the same in the two ecological areas, the important pollinator species are different. In aspen parkland, log-nesting species of leaf-cutter bees are important (Knowles 1943; Peck and Bolton 1946), whereas in mixed prairie the important species are ground-nesting in habit (Sladen 1918; Salt 1940; Hobbs 1950).

Scattered throughout the mixed prairie region of southern Alberta are the microhabitats of the river valleys and irrigated areas. These treed areas more closely resemble aspen parkland than mixed prairie. Some of the log-nesting species of *Megachile* that are abundant in the parkland regions of Western Canada are also found in the treed river valleys and irrigated areas. But there is seldom sufficient moisture to initiate rot in fallen trees in the mixed prairie region and therefore the species that prefer this type of nesting habitat are few in number of individuals. Those species that tunnel into the soil are restricted by cultivation and irrigation but the large areas of range land that, in many cases, surround the irrigated areas provide unlimited nesting sites. Species that rely on hollow-stemmed plants for nesting sites must also be uncommon because of the lack of perennial shrubs such as sumac or of weeds like mullein in the region. For the above reasons, a common species that is peculiar to mixed prairie and whose nesting habits are not known is likely to be a ground-nester.

During this study it was found that certain species of *Megachile* were important pollinators of alfalfa. This paper is a report on an ecological study of each of the leaf-cutter species that occur in southern Alberta.

Grateful appreciation is extended to Dr. C. W. Farstad, Officer-in-Charge, Field Crop Insect Section, and to Dr. W. C. Broadfoot, Director, Science Service Laboratory, Lethbridge, for their advice and encouragement; to Dr. H. A. Scullen, Oregon State College, for his constructive criticism and suggestions; to Dr. R. Lambert, Systematic Entomology Unit, Division of Entomology, Ottawa, for the determination of insects in genera other than *Bombus* and *Megachile;* to Dr. E. H. Moss and Mr. J. A. Campbell, University of Alberta, and Mr. J. J. Sexsmith, Canada Experimental Station, Lethbridge, for identification of certain flowering plants; to Messrs. N. E. Kloppenborg and W. J. Fruet, Lethbridge laboratory, for the photographs; to Mr. Dale Cox, Scandia, Alberta, for his assistance and the use of his alfalfa fields; and to Mrs. Elizabeth Hobbs, for the discovery of the nesting sites of several species of *Megachile*.

METHODS AND PROCEDURES

Muesebeck's *et al.* catalog (1951) was followed in applying subgeneric, specific, and subspecific names. Species of *Megachile* and *Bombus* were identified by the writers.

The relative importance of each species of *Megachile* was assessed on the basis of Alberta distribution, *frequency* and *abundance* in mixed prairie, pollen preferences of females, nesting habits, and flight period.

Data on distribution, frequency, abundance, and

pollen preferences were obtained from survey records and field notes. When a specimen was captured, place, date, and pollen preference were recorded on the labels, which were pinned beneath it. Microhabitat was considered when place was being recorded.

The Alberta distribution of each species was plotted on a map (Fig. 1), on which was superimposed a line separating that area designated by Coupland (1950) as mixed prairie. Records from Mitchell (1935a, 1935b, 1936, 1937a, 1937b, 1937c), Sladen (1918), the University of Alberta collection, Edmonton, and the Lethbridge laboratory collection were distinguished. Each species is recorded as having been found in one or more of 3 ecological areas: (a) mixed prairie, (b) fescue grassland, and (c) aspen parkland.

The locations within the mixed prairie of southern Alberta at which a species had been taken were counted to obtain the *frequency*.

A species was considered abundant if more than 100 specimens were recorded from mixed prairie; common, 50 to 100; and rare, fewer than 50. When a species was abundant and could be identified in the field it was noted but not captured. Rare species were captured whenever they were seen. Hence, the figures for the abundant species are low.

Although males of *Megachile* spp. trip alfalfa flowers occasionally, they do not excavate tunnels, make leaf-cuttings, or gather pollen to provision cells. Tripping of alfalfa flowers by female leaf-cutter bees is a deliberate act, the prime factor in their visits being the gathering of pollen for the provisioning of the cells. Hence, only records pertaining to females are considered. Those from Knowles (1943), Mitchell (1935a, 1935b, 1936, 1937a, 1937b, 1937c), Peck and Bolton (1946), Sladen (1918), and Stevens (1949) that could be definitely linked with female specimens are also considered when fidelity of a species to a particular flower or group of flowers is being considered.

Study has shown that even when lists of flower records are linked only with females they may be misleading. If a species of plant is absent from the area the bee will utilize another species. A preferred source early in the season may be abandoned for another source later on. Therefore, when pollen preferences were recorded, flowering plants growing close to the host plant were also noted.

Data on nesting habits were compiled from the literature and the writers' field notes. Dead stalks of pithy- and hollow-stemmed forbs and rotten logs were examined for nests. Holes with diameters of ¼, ⅜, and ½ inches were bored in logs to attract females of log-nesting and stem-inhabiting species.

An isolated chokecherry shrub, *Prunus virginiana* L., on the bank of the Bow River near Scandia, Alberta, and the only major leaf-cutting source within half a mile, provided an opportunity to study the ground-nesting species *M. perihirta*. Data on nesting habitat and flight period were secured at or near this shrub.

By sitting quietly in a likely looking locale, the writers could readily see the bees alighting with leaf-cuttings at their tunnel entrances.

In 1950, the numbers of bees leaving the shrub with leaf-cuttings in a five-minute period were counted. In 1951 and 1952, ten-minute counts were made, and were halved so that the three curves would have the same ordinates (Figs. 2, 3, 4). In all years, counts were made twice per day and an average was calculated. Counts were commenced soon after the date on which the first leaf-cuttings were noted, and were continued, whenever possible, until activity at the shrub ceased.

To obtain beginning, peak, and end of flight activity for *M. dentitarsus,* a close watch for emergence of males followed by observation of female activity in alfalfa fields was made.

Data on the number of generations were secured mostly from a close examination of captured specimens, supplemented with emergence records from cells removed from nesting sites in the

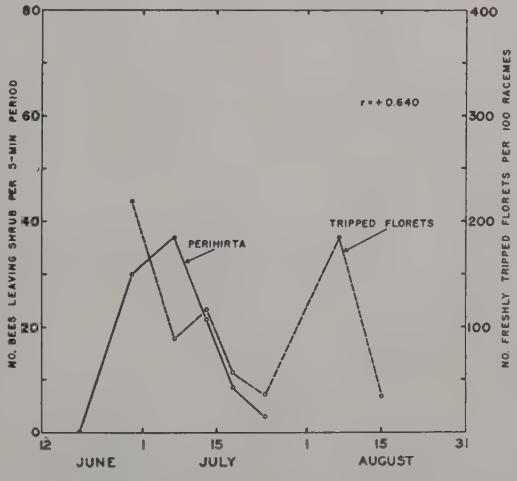

FIG. 2. Mean numbers of *M. perihirta* leaving the shrub with leaf-cuttings per 5-minute period, and numbers of freshly tripped flowers per 100 racemes, in 1950.

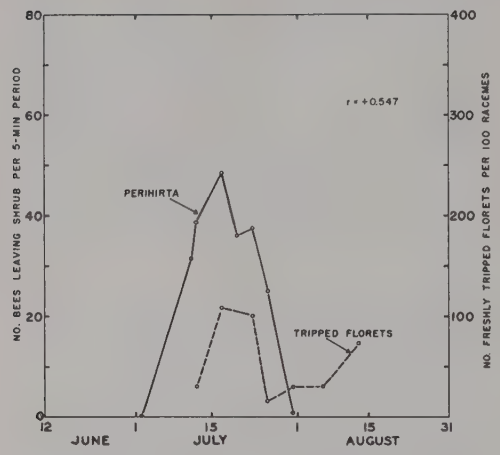

FIG. 3. Mean numbers of *M. perihirta* leaving the shrub with leaf-cuttings per 5-minute period, and numbers of freshly tripped flowers per 100 racemes, in 1951.

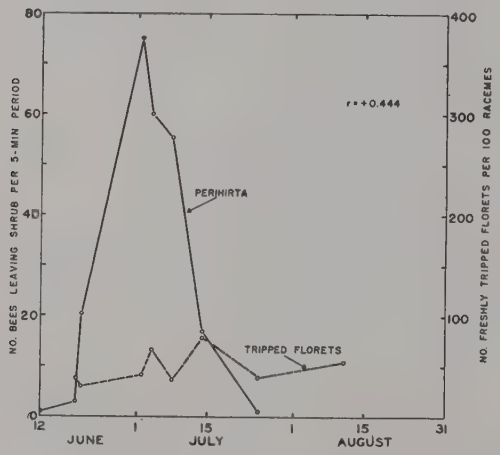

FIG. 4. Mean numbers of *M. perihirta* leaving the shrub with leaf-cuttings per 5-minute period, and freshly tripped flowers per 100 racemes, in 1952.

ground or rotten logs. Specimens taken after the main flight period of the species were considered members of a second generation if the margins of their wings were not torn and the hair on their bodies was long and abundant.

The relationship of flight activity to the amount of pollination taking place was determined by calculating the correlation coefficient for the amount of tripping (the number of freshly tripped flowers per 100 racemes in 1950 and 1951 and 200 racemes in 1952) and *M. perihirta* activity (the number of bees leaving the *Prunus* shrub in 5 minutes in 1950 and in 10 minutes in 1951 and 1952).

Counts of freshly tripped flowers per 100 racemes were made on an alfalfa field close to the bank of the river opposite the shrub. These were made during the interval between the first and second counts at the shrub. Because *Megachile* spp. seldom fly at temperatures below 67° F. (Peck and Bolton 1946) and the time taken for standard petals to begin folding varies (Tysdal 1940), the writers waited until the temperature had been above 67° F. for at least three hours before recording as freshly tripped flowers those on which the standard petals had not folded so as to even partially hide the sexual columns.

RESULTS

Alberta distribution, and frequency and abundance of *Megachile* spp. in mixed prairie are given in Table I. Data on their nesting habits along with those taken from the literature are given in Table II. Those on pollen preferences in the mixed prairie region of southern Alberta are recorded in Table III. In all cases the species of *Megachile* are listed in the approximate order of importance, this having been deduced from a consideration of all six criteria.

Data on the flight period of *M. perihirta* are shown in Figures 2, 3, and 4.

The first *dentitarsus* females were seen to trip alfalfa flowers about July 20, 1951, and peak numbers were observed on August 10. Flight activity had almost ceased by September 5. An activity curve from the above observations would be bimodal, because of a 13-day period of cold, rainy weather in late August and early September, during which flight activity was at a standstill. In

TABLE I. *Alberta distribution, and frequency and abundance of species of* Megachile *in southern Alberta.*

Species	Alberta distribution*	Frequency in mixed prairie	Abundance in mixed prairie	
		No. of localities from which species is recorded	No. of specimens recorded	Category
dentitarsus Slad.	a	17	279	Abundant
perihirta Ckll.	a, b	17	158	Abundant
brevis Say	a	8	18	Rare
melanophaea Sm.	c, b, a	11	23	Rare
frigida Sm.	c, b, a	6	63	Common
latimanus Say	a, b	2	2	Rare
cleomis Ckll.	a	2	2	Rare
relativa Cress.	c, b, a	4	16	Rare
montivaga Cress.	c, b, a	3	4	Rare
inermis Prov.	c, b, a	1	2	Rare
pugnata Say	c, b, a	1	6	Rare
wheeleri Mitch.	a, b	11	142	Abundant
parallela Sm.	a	3	15	Rare
anograe Ckll.	a	3	3	Rare

*By ecological areas in order of importance: (a) mixed prairie, (b) fescue grassland, (c) aspen parkland.

TABLE II. *Nesting habits of species of* Megachile *that occur in southern Alberta.*

Species	Nesting habits	
	Site(s)	Material(s)
dentitarsus	ground*.	cuttings from *Rosa*, *Prunus*, *Salix* sp(p).*
perihirta	ground* (Hicks 1926, Sladen 1918)	cuttings from *Rosa*, *Prunus*, *Salix*, *Convolvulus*, *Rumex*, *Elaeagnus* sp(p).*
brevis	ground (Hicks 1926, Mitchell 1935a), rolled leaves of plum?, sumac stem?, corn (Mitchell 1935a)	cuttings from *Rosa* sp(p).*, rose petals and leaves (Hicks 1926), yellow petals (Mitchell 1935a)
melanophaea	ground (Graenicher 1905),	cuttings from *Rosa* sp(p).*
frigida	rotten *Populus* logs*, rotten log (Mitchell 1935b)	cuttings from *Salix*, *Polygonum*, *Epilobium* sp(p).*
latimanus	ground (Mitchell 1936)	cuttings from oak? (Mitchell 1936)
cleomis	ground (Hicks 1926)	rose leaves (Hicks 1926)
relativa	tunnel in bank (Hicks 1926), logs? (Mitchell 1935b), sunflower stems? (Peck & Bolton 1946)	poplar and rose leaves (Peck & Bolton 1946)
montivaga	old mullein and sunflower stems (Hicks 1926)	petals and pith (Hicks 1926)
inermis	decaying wood (Sladen 1919), holes bored in logs (Peck & Bolton 1946)	poplar leaves (Peck & Bolton 1946)
pugnata	rotten logs*	
wheeleri	ground†	cutting *Rosa* sp.*
parallela	ground (Fischer 1951)	entire leaves of *Spiraea vanhouttei* and *Trifolium repens* (Fischer 1951)
anograe	ground†	

*Observed by the writers.
†Assumption(s) based on knowledge of distribution and habitat.

TABLE III. *Pollen preferences of females of* Megachile *spp. in the mixed prairie region of southern Alberta.*

Species	Number of Records												
	Alfalfa	Sweet clover	Prairie clover	Other legumes	Gumweed	Sunflower	Sow thistle	Canada thistle	Golden aster	Other composites	Fireweed	Tumbling mustard	Other plants
dentitarsus	76	2	7	0	16	6	0	0	3	0	0	0	0
perihirta	25	2	0	0	0	0	0	5	6	2	1	7	3
brevis	10	1	0	0	1	0	0	0	0	0	1	0	0
melanophaea	10	2	0	0	0	0	0	0	0	0	0	0	2
frigida	8	0	0	0	0	0	0	0	0	0	18	0	0
relativa	1	0	0	0	0	0	0	1	0	1	4	0	0
montivaga	0	0	0	0	0	0	0	0	0	0	2	0	0
pugnata	0	0	0	0	1	0	0	0	0	0	0	0	0
wheeleri	0	0	0	0	71	0	0	0	1	5	0	0	0
parallela	0	0	0	0	4	4	1	0	0	0	0	0	0
anograe	0	0	0	0	0	0	0	0	0	0	1	0	1

1952 the flight period of *dentitarsus* began on or about July 8. The upswing after August 1 in the curves representing the numbers of freshly tripped flowers per 100 racemes is considered due to *dentitarsus* activity (Figs. 2, 3, 4).

There was a positive correlation of 0.640 in 1950, 0.547 in 1951, and 0.444 in 1952 between the number of bees leaving the *Prunus* shrub and the amount of tripping taking placed in the field (Figs. 2, 3, 4).

No species of *Megachile* emerges before alfalfa comes into bloom in southern Alberta. There is

usually only one generation per season and, even with the earliest-emerging species, the number of individuals of the second generation is small and most of those that emerge are males.

Discussion

Before much was known about the bionomics of species of *Megachile,* taxonomists had split the genus into several subgenera on morphological affinities. In most cases these affinities seem to have a bearing on nesting habits and pollen preferences. Hence, species that belong to the same subgenus are discussed together.

Subgenus *Xanthosarus* Rob.

This subgenus contains the most important group of alfalfa-pollinating species in the mixed prairie region of southern Alberta. Their distribution is restricted to mixed prairie or fescue grassland, indicating that they are ground-nesting in habit. Sladen (1918) found *perihirta* nesting in a newly built gravel road at Invermere, B. C. Hicks (1926) has found it nesting in the ground and observed the excavation of a tunnel. The writers have found their nests within a few feet of each other (Fig. 5), but *perihirta* is not considered gregarious in the same sense as species of *Nomia* or *Anthophora.* Although the prairie exhibits the same cover near the leaf-cutting source as it does as far as can be seen, and although some members of the species excavate tunnels near this source, many build their nests more than a quarter of a mile from it. Typical microhabitat is illustrated in Figure 6. Cells in excavated nests were found at the ends of unbranched tunnels that entered the ground at about a 60° angle and then ran parallel to and about two inches below the surface of the soil. An average of 3 cells per completed nest was calculated, the range being from 2 to 9. Nests observed by the writers were found either in gravelly areas on which widely spaced clumps of grass and sage were growing (Fig. 5) or in areas of light sandy loam that were thickly covered with clumps of *Bouteloua* sp(p). and *Stipa* sp(p). (Fig. 6.) The writers found some 35 nests, the tunnel entrances of which were at the bases of clumps of grass or pasture sage, *Artemisia frigida* Willd., in all but two cases. These two were between or under rocks.

On the basis of frequency and abundance of the species of the subgenus *Xanthosarus* in the alfalfa seed-growing regions of southern Alberta, *dentitarsus* is the most important of the three species. The eastern species, *latimanus,* reaches the western limits of its distribution in southern Alberta and is rarely encountered in any sector of the area. Although *perihirta* and *dentitarsus* have

Fig. 5. Two nesting sites of *M. perihirta* near bank of Bow River, Scandia, Alberta.

Fig. 6. Micro-habitat of typical *M. perihirta* nesting site, Scandia, Alberta.

been recorded from the same number of localities (Table I), the west coast species, *perihirta,* is rarely found in those areas of southeastern Alberta where the altitude is less than 2,300 feet. *M. perihirta* is considered the most important pollinator of alfalfa in southern British Columbia by Sladen (1918) and Buckell (1950). *M. latimanus* is highly regarded, by Peck and Bolton (1946) and Stevens (1949), as a pollinator of alfalfa in areas where it is abundant.

Pollen preferences show that *dentitarsus* exhibits a greater fidelity to alfalfa than does *perihirta* (Table III). The main competitor for the services of *dentitarsus* is gumweed, *Grindelia perennis* A. Nels., but it does not become a competitor until

late in the season. Peck and Bolton (1946) list sow thistle, *Sonchus arvensis* L., as the only competitor with alfalfa for the services of *latimanus*. Stevens (1949) listed many competitors but stated that *latimanus* visited alfalfa freely and regularly tripped the flowers. He reported that, from Dickinson westward in North Dakota, *dentitarsus* specimens were taken mostly from alfalfa. Until 1951 it was thought that *perihirta* exhibited the same fidelity to alfalfa as *dentitarsus,* but when excess rainfall produced flowers in abundance from the woody, perennial roots of golden aster, *Chrysopsis villosa* (Pursh.) Nutt., *perihirta* utilized this plant as a source of pollen in preference to alfalfa. Most of the cells of *perihirta* that were excavated and examined in 1951 contained *C. villosa* pollen. The succeedingly lower values for the correlation coefficients (Figs. 2, 3, 4) are considered due to the increasing competition of native prairie flora, especially *C. villosa.* It also collected pollen from tumbling mustard, *Sisymbrium altissimum* L., that was growing close to alfalfa. Neither species is attracted to sweet clover when alfalfa is in bloom in the area.

Since Hobbs (1950) reported on the bionomics of *dentitarsus,* it has been found that he was dealing with a species complex made up of the early-emerging *perihirta* and the late-emerging *dentitarsus.* The flight period attributed to *dentitarsus* is now known to be that of *perihirta.* One important reason why *perihirta* might be listed as being more important than *dentitarsus* as a pollinator of alfalfa is that its flight period occurs earlier, allowing the flowers that it trips and cross-pollinates time to set mature seed.

There is only one generation of *dentitarsus.* Although *perihirta* has a partial second generation, it appears too late to be of much use as a pollinator of alfalfa.

Subgenus *Litomegachile* Mitchell

Two species of this subgenus, *brevis* and *cleomis,* are peculiar to mixed prairie (Table I) in Alberta. Neither was recorded by Knowles (1943) or Peck and Bolton (1946) from nothern Saskatchewan. In Mitchell's (1935a) review of literature *brevis* has been recorded as having built nests in burrows in the ground, in rolled leaves of a plum tree, in a sumac stem and railroad tie, and "on corn." Because species of *Litomegachile* are closely related and variable, he thought that the determination of some of the specimens with which these records were linked may have been wrong. The specimen that was found to nest in the ground and the one that made its nest on corn were identified by Mitchell (1935a) as *brevis.* Hicks (1926) observed a female of *cleomis* nesting in the ground. If *brevis* can utilize the various types of nesting habitats attributed to it, its Alberta distribution is not limited by a lack of nesting sites. It is likely that *brevis* and *cleomis* have reached the northern limits of their distribution at this particular latitude, longitude, and altitude. *M. brevis* is one of the smallest and most fleeting species of leaf-cutter bees occurring in southern Alberta. It is therefore likely that its numbers are greater and that it is more important than is thought.

Female specimens of *M. brevis* that could be definitely linked with flower records by Mitchell (1935a) indicate that this species has a wide range of pollen preferences. The writers' records (Table III) and Sladen's (1918) observations indicate that it prefers alfalfa. Little is known about pollen preferences of *cleomis.* Stevens (1949) records it from sweet clover and prairie clover, *Petalostemon* spp., but does not report the sex of the specimens. Two records from Mitchell (1935a) can be definitely linked with females. These are from hollyhock, *Althaea* sp., and milkweed, *Asclepias* sp.

M. brevis is probably the first species of *Megachile* to appear, emerging about the time alfalfa comes into bloom. The beginning of the flight period of *cleomis* is not known.

Subgenus *Delomegachile* Viereck

M. melanophaea s. str. and *frigida* s. str. have almost identical distribution records in Alberta. Both are widely distributed throughout the aspen parkland. Both have approximately the same distribution in mixed prairie but, whereas all specimens of *frigida* have been taken from areas where log nesting-sites were to be found in the vicinity, specimens of *melanophaea* have been captured on prairie where none could be seen. The greater frequency (Table I) may indicate that *melanophaea* is not as limited by nesting habitat as is *frigida.* Graenicher (1905) found *melanophaea wootoni* Ckll. nesting in the soil as did Hicks (1926). (Dr. T. B. Mitchell, North Carolina State College of Agriculture and Engineering, Raleigh, has informed the writers that the species identified by Graenicher as *melanophaea* is its subspecies *wootoni.*)

The importance of *melanophaea* [= *calogaster* Ckll.] in southern Alberta is based more on Sladen's (1918) appreciation of it than on what the writers have seen. Mitchell (1935b) has recorded females of *melanophaea* from alfalfa in the mixed prairie regions of Alberta and Montana, and Mr. H. L. Seamans, formerly Officer-

in-Charge, Field Crop Insect Section, Lethbridge, Alberta, collected females on alfalfa in southern Alberta in 1922-23. Ten specimens have been recorded from alfalfa and only 2 from sweet clover (Table III). One on sweet clover could have been gathering alfalfa pollen and most of the 10 recorded from alfalfa could have been on sweet clover. The two specimens on other plants were taken where neither sweet clover nor alfalfa was growing. Flower records that could be linked with females from Mitchell (1935b), Peck and Bolton (1946), Sladen (1918), and Stevens (1949) also indicate that alfalfa is a preferred source. Its flight period is about 10 days earlier than that of *perihirta* and, if it were more common in southern Alberta, it would be a valuable pollinator of early bloom.

M. frigida is the most important pollinator of alfalfa in the aspen parkland, according to Knowles (1943) and Peck and Bolton (1946). It is log-nesting in habit and has been found nesting gregariously in rotten logs in the irrigated districts of the mixed prairie. On June 29, 1948, the senior author's wife found a rotten log in which at least three females were nesting gregariously. When the log was split open, 51 cells were removed. Peck and Bolton (1946) attempted to increase its numbers in the alfalfa seed-growing regions of northern Saskatchewan by boring holes in logs, but when emergence took place from the holes, which had been utilized by leaf-cutter bees, *frigida* was not present. Although this species is found in all of the older, treed areas on mixed prairie it is not abundant. This is probably due to a lack of the rotten logs that serve as nesting sites.

M. frigida has not been seen to gather pollen from alfalfa in the seed-growing areas of southern Alberta. In these areas it is almost always found on fireweed, *Epilobium angustifolium* L. On an experimental field in an isolated river valley where no fireweed was present, *frigida* was an important cross-pollinator of alfalfa.

If fireweed were eliminated and nesting sites were made available it might become a valuable species in the mixed prairie region. Its flight period, like that of *perihirta*, begins soon after alfalfa comes into bloom. There is an insignificant, partial second generation in favorable years.

Subgenus *Megachile* Latreille

All three species that occur in southern Alberta, *relativa*, *montivaga*, and *inermis*, are found in both the mixed prairie and aspen parkland, *relativa* and *inermis* having a greater frequency in the parkland region. *M. montivaga* is not common in either ecological area. In the mixed prairie region all are restricted to the treed areas of the river valleys and irrigated areas, indicating that they are log-nesters. All are rarely found in the restricted areas on mixed prairie where they occur.

It is likely that fireweed is the chief competitor of alfalfa for the services of these species (Table III). Peck and Bolton (1946) collected 20 females of *relativa* on *Epilobium* sp. as compared with 8 on alfalfa. *M. montivaga* is recorded only from fireweed (Table III), and *inermis* has been recorded from fireweed by Knowles (1943). Peck and Bolton (1946) took twice as many of *inermis* on fireweed as on alfalfa. Composites, including perennial sow thistle, are also preferred pollen sources of *inermis* and *relativa* (Peck and Bolton 1946).

At present none of the species of the subgenus *Megachile* can be rated as a valuable pollinator of alfalfa in southern Alberta. *M. relativa* is the most frequent and abundant of the three (Table I). Only 1 female has been taken on alfalfa in this area (Table III), but further knowledge of its bionomics may lead to its increase and utilization for pollination of alfalfa.

Subgenus *Argyropile* Mitchell

The Alberta distribution of *parallela* is limited to mixed prairie. Its frequency is low and it is rarely found (Table I). It too has probably reached the northern limits of its distribution. *M. parallela* has been found by Fischer (1951) to be ground-nesting in habit.

Its flight period coincides with the blooming of the composites *Helianthus* sp(p). and *Grindelia perennis*. Except for 8 specimens that were taken on an isolated, experimental alfalfa field where competing growth had been reduced to a minimum with 2, 4-D, it has not been recorded from any plant other than a composite (Table III) in southern Alberta. Mitchell (1937b) records it from sweet clover as well as from composites. Its flight period, which begins the last week in July and ends early in September, is too late even if it could be induced to gather pollen from alfalfa.

Subgenus *Sayapis* Titus

M. pugnata s. str. is the only member of this subgenus that occurs in southern Alberta. It is distributed throughout both the parkland and mixed prairie regions, being more frequent and abundant in the parkland areas. In the mixed prairie area it is restricted to the treed river valleys and irrigated areas and is rare in these areas (Table I).

Its distribution suggests that it is a log-nester.

No reference to its nesting habits was found in the literature.

Although this species flies at a time when it would be of use as a pollinator of alfalfa, it, too, is a lover of composite flowers. The only legume in southern Alberta from which it has gathered pollen is sweet clover (Table III). Peck and Bolton (1946) recorded equal numbers from perennial sow thistle and dandelion, *Taraxacum officinale* Weber.

Subgenus *Xeromegachile* Mitchell

M. manifesta Cress. was listed with 4 other species by Sladen (1918) as a pollinator of alfalfa in southern Alberta, and Mitchell (1937a) records it from Calgary. These are the only published records of the species from Alberta, and the writers did not take it during their research. Neither is it recorded in Buckell's (1950) list of British Columbia species or in the Lethbridge laboratory collection. Moreover, specimens of *wheeleri,* some of which were identified by Mitchell, now in the Canadian National Collection represent the material on which Sladen based his records of *manifesta* from Medicine Hat and Lethbridge, Alberta (personal communication from Dr. R. Lambert, Systematic Entomology Unit, Entomology Division, Ottawa). This is the only record of *wheeleri* on alfalfa.

M. wheeleri Mitchell is probably the most abundant species of leaf-cutter bee in the mixed prairie region. Its abundance as given in Table I is underrated. It was observed on gum-weed on many occasions but was not collected. It may be restricted to sandy areas, but wherever the species is found, large numbers of it may be seen. Mitchell (1937a), in his summary of the habits of species of this subgenus, stated that most of the species appeared to be adapted to sandy, arid regions and depended upon a narrow range of flowers. He felt that this food limitation had resulted in a shortening of the flight period and the geographical localization of many of the species. It is confined to the mixed prairie and its flight period coincides with the blooming of gum-weed. Its nests have not been found and identified but it is also thought to be a ground-nester.

Large series have been taken on *Grindelia perennis* and smaller numbers on *Solidago* sp(p). by the writers (Table III). Even if it could be induced to gather pollen from alfalfa its flight period is so late that its services would be of little use.

Subgenus *Derotropis* Mitchell

M. anograe is the only species of this subgenus that has been taken in southern Alberta. It was not recorded until 1952, when 3 specimens from 3 different localities were collected by the writers (Table I). It has not been recorded from alfalfa. Mitchell (1936) records one female from *Astragulus* sp. The writers took it on fireweed and spiderflower, *Cleome serrulata* Pursh. (Table III.)

Little is known about this species. The male has not been associated with the female (Mitchell 1936). Its nesting habits are not known. Even if it preferred alfalfa to other plants, it is too rare to be of value in this region.

Summary and Conclusions

The importance of each of the 14 species of *Megachile* that occur in the alfalfa seed-growing region of southern Alberta was determined by the following criteria: Alberta distribution, frequency and abundance in mixed prairie, nesting habits, pollen preferences, and flight period.

Those species whose distribution is confined to mixed prairie, that are ground-nesting in habit, that prefer alfalfa pollen, and whose emergence coincides with the coming of alfalfa into bloom are the most important pollinators of alfalfa in southern Alberta. Under conditions such as exist at present, the ground-nesting species *M. dentitarsus* and *perihirta* are the most important pollinators in this area. *M. dentitarsus,* although its flight period is later than that of *perihirta,* is considered the more important because *perihirta* does not exhibit the fidelity to alfalfa displayed by *dentitarsus.* When the season is abnormally short, as in 1951, *perihirta* is more important.

Generally, the wider the distribution of a species the less important it is as a pollinator of alfalfa in the mixed prairie region.

Of the criteria, the most important is flight period because man has no control over it. It is difficult to increase the abundance of species that have reached the outer limits of their distribution in southern Alberta. It is theoretically possible to increase the frequency and abundance of all other species by providing nesting sites, materials for nest construction, and food sources. Efficiency would be increased by planting alfalfa fields and leaf-cutting sources close to nesting sites.

In determining the value of *Megachile* spp. as pollinators of alfalfa, only flower records (pollen preferences) for females should be considered. These should include all plants in flower in the area where the bee is gathering pollen.

References

Bohart, George E. 1951. Alfalfa seed growers of Utah should protect their wild bees. Farm and Home Sci., **12**: 32-33, 37.

Buckell, E. R. 1950. Records of bees from British

Columbia: Megachilidae. Proc. Ent. Soc. British Columbia, **46**: 21-31.

Carlson, J. W. et al. 1950. Growing alfalfa for seed in Utah. U.S.D.A. Cir. 125.

Coupland, Robert T. 1950. Ecology of mixed prairie in Canada. Ecol. Monogr., **20**: 271-315.

Fischer, Roland L. 1951. Observations on the nesting habits of megachilid bees. Jour. Kans. Ent. Soc., **24**: 46-50.

Graenicher, S. 1905. Some observations on the life history and habits of parasitic bees. Wisc. Nat. Hist. Soc. Bul., **3**: 153-167.

Gray, H. E. 1925. Observations on tripping alfalfa blossoms. Canad. Ent., **57**: 235-237.

Hicks, Charles H. 1926. Nesting habits and parasites of certain bees of Boulder County, Colorado. Univ. Colo. Stud., **15**: 217-252.

Hobbs, G. A. 1950. Pollinating species of bees in the irrigated regions of southern Alberta. Rpt. Twelfth Alfalfa Improvement Conf., Lethbridge, Alberta, Canada, pp. 47-49. [Processed.]

Knowles, R. P. 1943. The role of insects, weather conditions, and plant character in seed setting of alfalfa. Sci. Agr., **24**: 29-50.

Mitchell, Theodore B. 1935a. A revision of the genus *Megachile* in the Nearctic region. Part II. Morphology of the male sternites and genital armature and the taxonomy of the subgenera *Litomegachile, Neomegachile* and *Cressoniella* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **61**: 1-44.

———. 1935b. A revision of the genus *Megachile* in the Nearctic region. Part III. Taxonomy of subgenera *Anthemois* and *Delomegachile* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **61**: 155-205.

———. 1936. A revision of the genus *Megachile* in the Nearctic region. Part IV. Taxonomy of subgenera *Xanthosarus, Phaenosarus, Megachiloides* and *Derotropis* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **62**: 117-166.

———. 1937a. A revision of the genus *Megachile* in the Nearctic region. Part V. Taxonomy of the subgenus *Xeromegachile* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **62**: 323-382.

———. 1937b. A revision of the genus *Megachile* in the Nearctic region. Part VI. Taxonomy of subgenera *Argyropile, Leptorachis, Pseudocentron, Acentron* and *Melanosarus* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **63** 45-83.

———. 1937c. A revision of the genus *Megachile* in the Nearctic region. Part VII. Taxonomy of the subgenus *Sayapis* (Hymenoptera: Megachilidae). Trans. Amer. Ent. Soc., **63**: 175-206.

Muesebeck, C. F. W., K. V. Krombein, and H. K. Townes. 1951. Hymenoptera of America north of Mexico. Synoptic catalog. U.S.D.A. Agr. Monogr. No. 2. Washington, D. C.

Peck, O., and J. L. Bolton. 1946. Alfalfa seed production in northern Saskatchewan as affected by bees, with a report on means of increasing the populations of native bees. Sci. Agr., **26**: 388-418.

Salt, R. W. 1940. Utilize wild bees in alfalfa seed production. Canada Dept. Agr., Div. Ent., F.C.I.I. processed leaf. 266.

Sladen, F. W. L. 1918. Pollination of alfalfa by bees of the genus *Megachile*. Table of Canadian species of the *latimanus* group. Canad. Ent., **50**: 301-304.

———. 1919. Notes on Canadian representatives of British species of bees. Canad. Ent., **51**: 124-130.

Stevens, O. A. 1949. Native bees. N.D. Agr. Exp. Sta. Bimonthly Bul., **11**: 130-135.

Tysdal, H. M. 1940. Is tripping necessary for seed setting in alfalfa? Jour. Amer. Soc. Agron., **32**: 570-585.

POLLEN STUDY OF TWO BOGS IN TEXAS[1]

J. E. Potzger and B. C. Tharp

Department of Botany, Butler University, Indianapolis, Indiana, and Department of Botany, University of Texas, Austin, Texas

In 1943, the authors reported up to five per cent spruce and fir pollen from the Patschke Bog in Texas. Since that time, pollens of these same boreal genera have also been found by Frey (1951) in North Carolina and by Wilson (see Davis) (1946) in Florida. Further pollen studies are in progress in the latitudes just referred to and through the work of Deevey (1944) and Sears (1952) pollen studies have been pushed southward into Mexico.

The two Texas bogs considered in the present study are located a short distance north from the Patschke Bog in Milam and Robertson counties. In the Gause Bog, pollens of spruce and fir totalled up to eleven per cent (Fig. 1) in the lowermost foot-level, thus adding to the accumulating evidence of a wide-spread cool-moist climate, and migration of boreal genera far to the south of the actual borders of continental ice caps.

Methods

The borings were made under direction and supervision of B. C. Tharp. A Hiller-type borer was used. The samples were placed into properly labelled vials, securely stoppered, and sent to the second author for analysis. Samples which could be deflocculated easily were prepared according to the Geisler (1936) alcohol method. Compacted

[1] This is Publication 269 from the Botanical Laboratory of Butler University. For the photomicrographs of pollen grains (Fig. 2) we are indebted to Mr. G. K. Guennel, Paleobotanist, Coal Section, Indiana Geological Survey. For preparation of Figure 1 we express our thanks to Mrs. Margaret Esther Potzger.

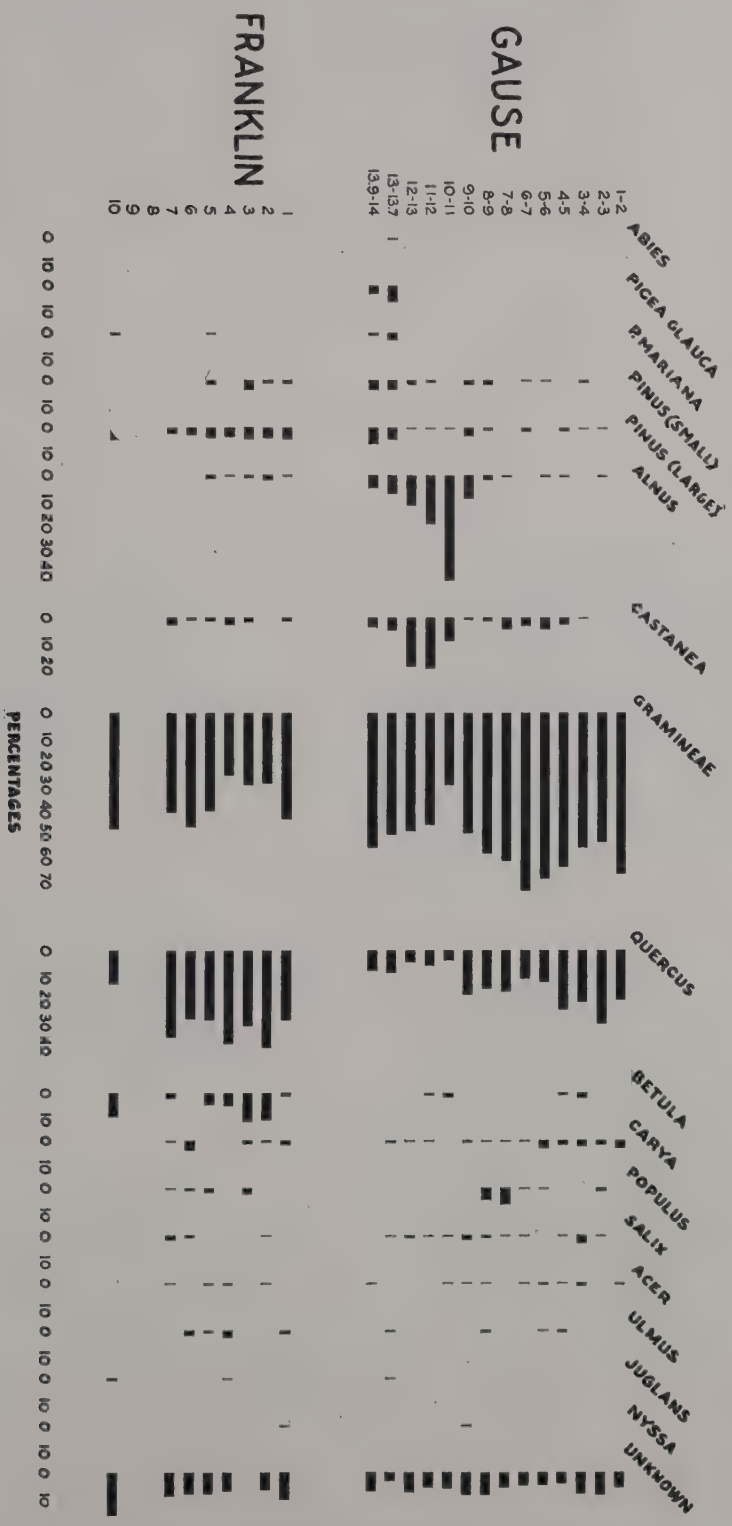

FIG. 1. Pollen profiles from Gause and Franklin bogs, Texas.

samples were placed into vials together with a small amount of KOH and boiled for several minutes. The procedure is similar to the one described by Erdtman (1943). Each sample was washed at least six times, allowing sediments to settle completely between washings. After the final washing the vial was filled with 95 per cent alcohol, and two drops of one per cent gentian violet was added as stain. A small amount of the sediment was placed on a slide and when the solution had dried to a moist state, warm glycerine jelly was mixed with it. From this supply, permanent slides were prepared for a count of 200 pollen grains at each foot level. Figure 1 presents the importance of the various genera in terms of percentages of the total count. Figure 2 presents photomicrographs of some spruce and fir pollens, and of the two types of pine, designated on Figure 1 as "small" and "large" pines. The spruce and fir pollens are from Gause Bog and the pine pollens are from the Franklin Bog.

Results

The profile from the Gause Bog in its gross features is almost a duplicate of that from the Patschke Bog (1947), except that the alder-chestnut period is more pronounced in the Patschke Bog. The profile from the Franklin Bog (Fig. 1) lacks the vegetational history from the cool-moist spruce-fir time to the warm-moist chestnut-alder period. This strongly suggests truncation of lower levels due perhaps to delayed bog formation. Beyond the alder-chestnut period, vegetational history is very similar in the two bogs. Associating, therefore, regional history of vegetation with the Gause Bog profile we have essentially the same successional trends as at the Patschke Bog, one county southward. In the lowermost levels,

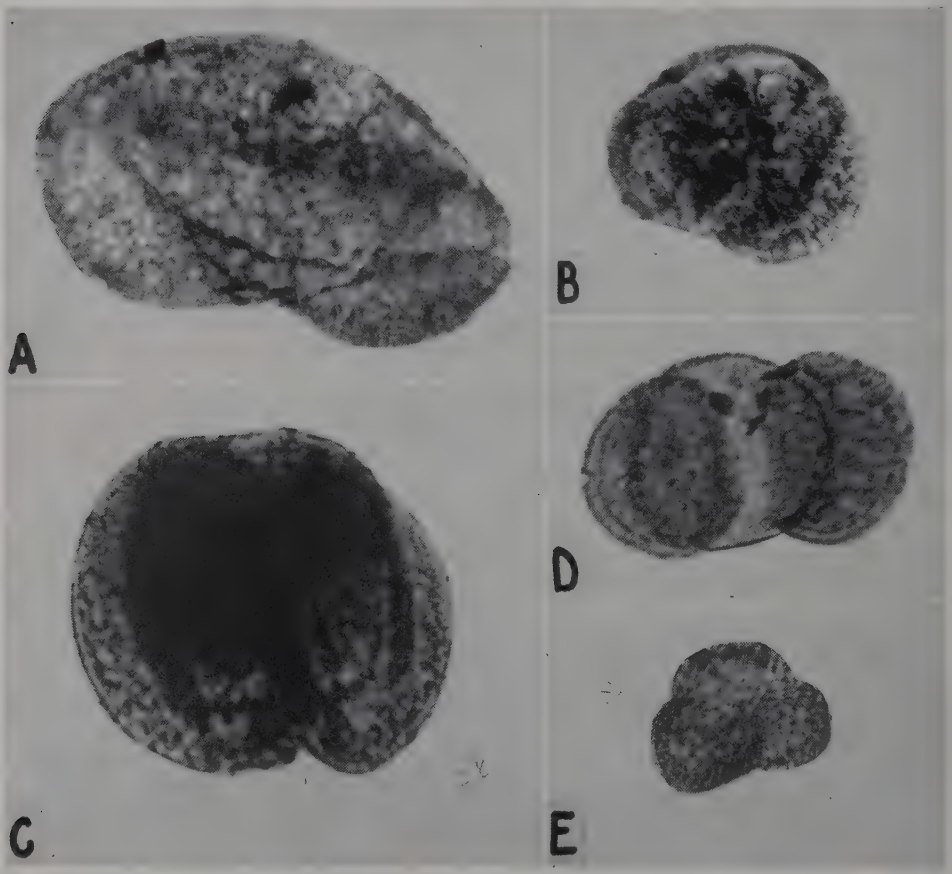

Fig. 2. Pollens of conifers from Texas bogs. A. *Picea glauca* (Moench) Voss B. *Picea mariana* (Mill.) BSP. C. *Abies* D. *Pinus* (large, 78 microns) E. *Pinus* (small, 44 microns)

spruce and fir are associated with abundant grasses. The boreal conifers disappear after the lowermost foot-level and grasses assume chief importance. Gradually alder and chestnut depress grasses to half their former abundance. The alder-chestnut peak persists for three-foot levels and then yields to invasion by oaks accompanied by a steep increase in grasses. This part of the vegetational history is identical in both bogs (Fig. 1). The grass-oak period persists to the topmost levels where hickory (*Carya*) shows a tendency to increase in abundance. The most significant difference between the two stations is that pine and birch (*Betula*) indicate greater abundance in the vegetation complex at the Franklin than at the Gause Bog. Compositae and ferns show nothing of diagnostic value. In the Franklin Bog, Umbelliferae increase strikingly in the topmost level. One pollen grain of *Drosera rotundifolia* L. was found in the 7-foot level of the Franklin Bog.

Discussion

The extensions of ranges of boreal genera and species far to the south of borders of Pleistocene ice caps are no longer viewed with the skepticism which met them a decade ago. Each new record strengthens the reliability of earlier reports. The hypothesis of long distance transport of spruce and fir pollens by wind is again ruled out by the fact that spruce and fir appear only in lowermost levels. Significant, too, is the fact that the Gause Bog brings the same distribution pattern as the Patschke Bog. There is little doubt that long distance transport of pollens by wind could account only for appearance of isolated and scattered pollen grains in a pollen profile. This opinion was also expressed by Dr. Nicholas Polunin in the discussion following his paper "Progress in Arctic aero-palynology" presented on the A.I.B.S. program in Minneapolis.

In a paper presented as a section of symposium on "The glacial border—climatic, soil, and biotic features," Potzger (1951) cited reports which showed that movement southward was not limited to plants but that such typical arctic animals as muskox and hairy mammoth also had pushed their range as far south as Texas and Florida.

In the interpretation of a limited number of pollen profiles from a given locality it is frequently very difficult to know if edaphic or major climatic controls are responsible for rise in abundance of pollen of given genera. This problem also presents itself in the present study. The greater abundance of pine and birch and also the higher ratio of oak to grass pollen in the Franklin Bog than in the Gause Bog may only represent microclimatic differences in the two localities. While such differences in vegetation induced by edaphic factors are difficult to cope with in studies of present-day vegetation, they frequently become a matter of speculation and conjecture when they find expression in unusual peaks in pollen profiles. A larger number of bogs from the same general region frequently modifies such differences by "tendency" characteristics.

In the present study, it seems hardly plausible that macroclimate differed greatly in two adjoining counties represented by the Gause and the Franklin bogs. Such local variation was pointed out by Guennel (1950) in the Merrillville Bog in Indiana where pine registered a very high peak in the closing three-foot levels. Here we know definitely that it was a record of local conditions, for a relic stand of white pine had persisted there until about 1945 when a fire eliminated it.

From the evidence at hand, it is, of course, impossible to ascertain during which period of Pleistocene dominance the intrusion into Texas by boreal life occurred. Antevs (1948) suggests Mankato glacial maximum. The same writer expressed the opinion that the climatic chronology at the Patschke Bog, thus also in the present bogs, is not well in agreement with the accepted chronology of central Texas northwestward to the State of Washington, but there is better agreement with that of northeastern North America. This is especially true for the profile from Singletary Lake in North Carolina. Frey (1951) lists four major climatic changes, *viz.* cool-moist (spruce and fir), warm-moist (hemlock and beech), warm-dry (oak), warm-moist (cypress, tupelo, sphagnum). One should point out that Frey took samples at more frequent intervals than we did in the Texas bogs and for that reason his closing warm-moist period may not be evident in the Texas bogs. Also, we do not know how much the surface layers of bogs may have been disturbed by fire and other cultural influences. There is also the possibility that increasing wetness along coastal areas may be an indication of rising sea level which is recognized in tidal marshes along the eastern coast. If *Sphagnum* cover can be interpreted as indicative of a more moist climate, then this can indeed be read into the *Sphagnum* cover at Patschke and other bogs in Texas.

Summary and Conclusions

1. The paper presents pollen profiles from Gause Bog (13.7 feet), Milam County, and Franklin Bog (10 feet), Robertson County, Texas.

2. At the 13.7-foot level of the Gause Bog eleven per cent of spruce and fir pollen was re-

corded. These boreal genera dropped out of the profile after that foot-level.

3. The Franklin Bog is very likely truncated at lower levels, for the cool-moist spruce-fir and the warm-moist alder-chestnut periods are wanting. Bog formation may have been initiated too late in the forest history to show these successions.

4. The vegetation is representative of the following climatic changes: cool-moist (spruce and fir), dry (grasses), warm-moist (alder and chestnut), warm-dry (grasses).

References

Antevs, Ernst 1948. Review of Patschke Bog. Jour. Geol. **56**: 83-84.

Davis, John Jr. 1946. The peat deposits of Florida. Geol. Bull. **30**. State of Florida, Dept. Conservation, Florida Geol. Surv. Tallahassee, Fla.

Deevey, Edward S., Jr. 1944. Pollen analysis and Mexican archeology. An attempt to apply the method. Amer. Antiq. **10**: 135-149.

Erdtman, G. 1943. An introduction to pollen analysis. Chronica Botanica Co., Waltham, Mass.

Frey, David G. 1951. Pollen succession in the sediments of Singletary Lake, North Carolina. Ecology **32**: 518-533.

Geisler, Florence 1936. A new method for separating fossil pollen from pea. Butler Univ. Bot. Stud. **3**: 141-146.

Guennel, G. K. 1950. History of forests in glacial Lake Chicago area. Butler Univ. Bot. Stud. **9**: 140-158.

Potzger, J. E. 1951. The fossil record near the glacial border. Ohio Jour. Sci. **51**: 126-133.

Potzger, J. E., and B. C. Tharp. 1943. Pollen record of Canadian spruce and fir from a Texas bog. Science **98**: 584.

———. 1947. Pollen profile from a Texas bog. Ecology **28**: 274-279.

Sears, Paul B. 1952. Palynology in southern North America. I. Archeological horizons in the basins of Mexico. Bull. Geol. Soc. Amer. **63**: 241-246.

TEMPERATURE REGULATION IN YOUNG PELICANS, HERONS, AND GULLS

GEORGE A. BARTHOLOMEW, JR.[1] AND WILLIAM R. DAWSON[2]
Department of Zoology, University of California, Los Angeles

Little is known about the capacity for temperature regulation in the young of large undomesticated birds, and no information exists which allows comparison of body temperatures of the young of large precocial and large altricial species under similar conditions in nature. The present study compares the body temperatures of the young of two altricial birds, the brown pelican (*Pelecanus occidentalis californicus*) and the great blue heron (*Ardea herodias treganzai*), and one precocial bird, the western gull (*Larus occidentalis livens*). All observations were made in rookeries at Puerto Refugio at the north end of Angel de la Guarda, a desert island located in the Gulf of California, Baja California, Mexico. The colonial nesting habits of the three species and the closeness of their rookeries made it possible to acquire data from a large number of individuals exposed to similar environmental conditions in an area which is characterized by extreme aridity, intense solar radiation, and high air temperatures.

[1] These studies were aided in part by a contract between the Office of Naval Research, Department of the Navy and the University of California (NR 160 171). The field activities were made possible through the generous cooperation of Joseph W. Sefton, Jr. of the Sefton Foundation who placed the facilities of the Research Ship Orca at our disposal.

[2] Public Health Service Research Fellow of the National Institutes of Health.

Methods

Observations and measurements were made on April 19, through April 23, 1953. Cloacal temperatures were taken with a quick-acting mercury thermometer inserted at least 2 centimeters. As indications of relative age we used the development of down and the length of the body from tip of bill to end of pygostyle with the bird in a prone extended position. Temperatures were measured during the morning and afternoon, and during the middle of the night. Air temperatures were taken with a shaded mercury thermometer held in the locations which were occupied by the young birds. The intensity of solar radiation was measured with black- and white-bulb thermometers consisting of thin copper spheres 4 inches in diameter fitted with mercury thermometers. The spheres, one painted flat black and the other painted flat white, were placed side by side in the direct sun in the rookery.

Brown Pelicans

Most of our observations were made in a rookery located on a sand-and-cobble spit rising about 10 feet above sea level at the south end of Granite Island which forms part of the east side of Puerto Refugio. The pelican nests were located on the tops of iodine bushes (*Allenrolfea*) which formed an irregular thicket three to six feet high (Fig. 1). At the time of our visit, the rookery contained

FIG. 1. California brown pelican rookery on Granite Island, Baja California, Mexico. Nests were constructed on the shrubs (*Allenrolfea*) in the foreground, which are 3 to 6 feet high, and in flat places among the granite boulders on the hillside shown in the background. The young pelicans in the center foreground are approximately 30 inches in length.

eggs and young ranging from newly hatched, naked nestlings, to downy individuals over 30 inches in length.

During our work in this rookery, the sky was completely clear and the solar radiation was intense (black-bulb temperature 51° C.). However, a brisk sea breeze held the daytime air temperature to from 24.2 to 26.6° C. The nighttime temperatures ranged from 16.1 to 16.6° C.

We divided the young into three age classes: naked (length, 6 to 12 inches), partly downy (length, 12 to 19 inches), and downy (length, 19 or more inches). The temperature data are summarized in Figure 2.

Naked young. During both day and night, the body temperatures of the naked birds were profoundly affected by environmental conditions. Exposure to the sun caused significant elevations in temperature, and exposure to the cool night air caused a conspicuous depression in body temperature. It was possible to determine directly the effects of solar radiation on the body temperature of naked young. The adults were very attentive to their newly hatched offspring and stayed on the nests until we approached to within 10 to 15 yards. We covered a number of recently hatched broods with cloth sun shields immediately after the adults left. Measurements of these shaded young gave data concerning the daytime body temperatures of the naked nestlings when shielded from insolation by the adults. Birds not thus protected were exposed to the full effect of solar radiation. A comparison of exposed and shielded birds is shown in Figure 2. Exposure to the direct rays of the sun for 7 to 22 minutes caused a mean elevation of approximately 3° C. in body temperature.

When exposed at night to moderately cool air temperatures, naked pelicans have little capacity for remaining warmer than the environment. Naked young exposed to an air temperature of 16° C. and measured within 20 minutes of the departure of their parents had a mean body tempera-

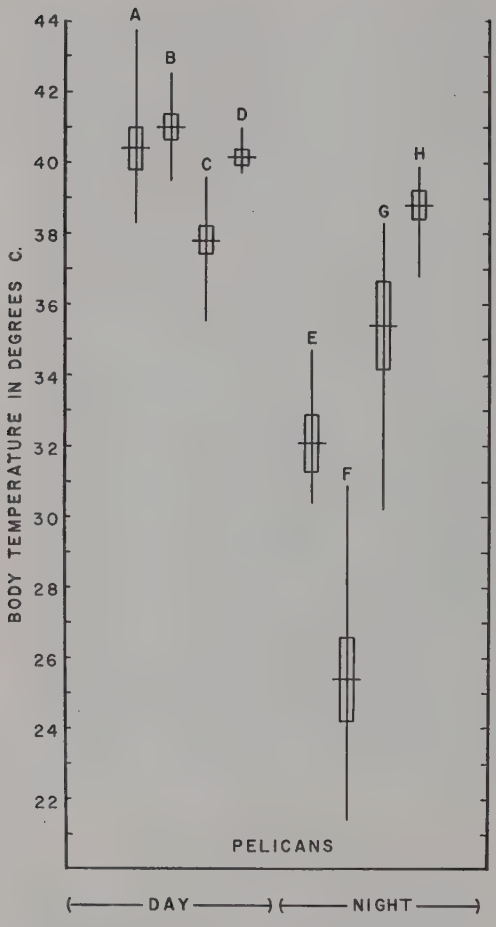

FIG. 2. Body temperatures of young California brown pelicans. The vertical lines indicate the range; the horizontal lines indicate the mean (M); and the rectangles indicate the interval $M + 2\sigma_M$ to $M - 2\sigma_M$. Units A-D: daytime body temperatures. Units E-H: nighttime body temperatures (2200-2400). A and B represent naked young exposed to direct sunlight during the morning (1030—black bulb temperature 41.5° C.) and during the afternoon (1330—black bulb temperature 51.0° C.), respectively. C represents naked young shaded from direct sunlight (1330). D represents downy young exposed to direct sunlight. E and F represent naked young that had been recently brooded and naked young that had not been brooded for at least 45 minutes, respectively. G and H represent partially downy young and downy young, respectively.

ture of slightly more than 32° C., whereas young of similar size measured 45 to 80 minutes after the departure of the adults had a mean temperature of only 25.4° C. (Fig. 2). Naked young were not torpid even at body temperatures almost 20° C. below the daytime resting level. Individuals with body temperatures between 21 and 22° C. vocalized spontaneously and appeared normally coordinated.

Downy young. The downy young exhibit well developed temperature regulation. During the day their temperatuers were relatively uniform (Fig. 2) with a mean of 40.1° C. The protection furnished to the young by their thick white down, their subcutaneous air sacs, and their capacity for vigorous gular fluttering enabled them to withstand the intense solar radiation and the moderately warm air temperatures without apparent stress and without shading by the adults. At night their temperatures were somewhat less uniform and averaged about 1.3° C. below the daytime level—a diurnal fluctuation comparable to that observed in adult chickens (Simpson 1910-1911) and adult mourning doves (Bartholomew and Dawson 1954).

Partly downy young. Brown pelicans 12 to 18 inches long are only partly covered by down. Their capacity to regulate body temperature in a cool environment was intermediate between that of the naked young and the completely downy young (Fig. 2).

Panting. Newly hatched naked young do not have a conspicuously enlarged gular pouch, and they appear to lack the ability for gular fluttering which is so characteristic of the downy young and adults of the genus *Pelecanus*. None of the young 7 inches or less in length exhibited gular flutter despite body temperatures elevated more than 3° C. above the daytime resting level. The gular fluttering of the downy young is as conspicuous as that of the adults, and it was observed only when the body temperature exceeded 40.0° C.

Development of homeothermy. The ability of young brown pelicans to maintain a high body temperature in a cool environment increases regularly with size until the young are 18 to 20 inches long (Fig. 3). Various factors contribute to this development of regulatory capacity. Among them are increase in mass; development of down; huddling by the older, better coordinated animals; and, presumably, changes in metabolic response to decreased temperature. None of the young brown pelicans shivered, although shivering in downy white pelicans (*Pelecanus erythrorhynchos*) has been reported (Bartholomew, Dawson, and O'Neill 1953).

Behavior and temperature regulation. The body temperatures of the naked and the partly downy young are regulated primarily by the adults which protect them from the sun and from the cool night air. The adults are very attentive to their naked

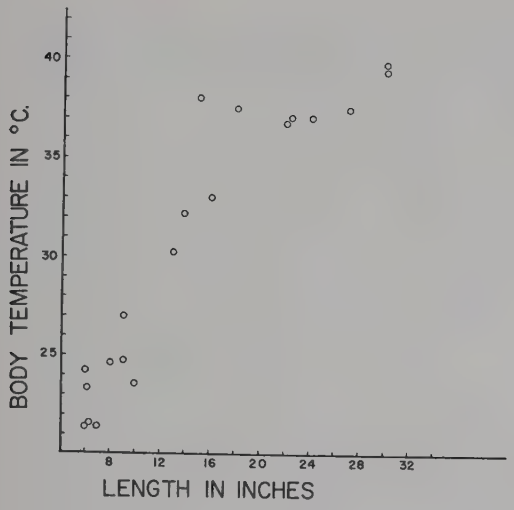

FIG. 3. Nighttime body temperatures of young California brown pelicans 45 to 80 minutes after departure of adults from the rookery, plotted against body length. 6-12 inches: naked individuals. 12-19 inches: partially downy individuals. 19 or more inches: downy individuals. Air temperatures 16.1-16.4° C.

nestlings; one parent or the other is ordinarily present at the nest at all times (Murphy 1936: 815).

The reluctance of the adults to leave their young was very conspicuous. They stayed on their nests even while we were working in the rookery; only those birds within about 40 feet of us took to the air. They flew only a short distance and returned to their nests within 45 seconds of the time we moved to another part of the rookery.

Because the larger young are able to tolerate intense solar radiation and prevent their body temperature from falling unduly at night, they are independent of parental attention except for food. All but the very largest of the young pelicans confined themselves closely to their nests and thus remained exposed to the sun unless shaded by their parents. The largest young wandered more freely and could seek shade under the iodine bushes. There were many nests scattered over the talus slopes of Granite Island some distance from the main rookery, and many of the larger young from these nests retreated during the hottest part of the day into crevices and small caves among the granite boulders (Fig. 4).

GREAT BLUE HERON

Observations on great blue herons were made in a rookery on the south shore of the west anchorage of Puerto Refugio. Their nests were sturdy platforms located 3 to 6 feet above the ground in an almost impenetrable thicket of iodine bushes growing in a level area 3 or 4 feet above high-tide line. A few of the nests were shaded, but most of them were exposed to direct insolation during the greater part of the day. The lower nests were shielded from the sea breeze, and consequently were subject to the highest air temperatures. Many of the nests held eggs as well as young, and most of the young were less than 10 inches long. Great blue herons are altricial, and the young when hatched are covered dorsally by long fine down which affords only slight protection.

Even at moderate air temperature (24.1-27.4° C.) a brief exposure to direct solar radiation caused significant elevations in body temperature. The comparison between exposed and shaded young, based on measurements taken within 40 minutes of the departure of the adults, is shown in Figure 5. When heated by the sun even the youngest herons fluttered the gular area powerfully about 4 times per second (see Wetmore 1921). Black bulb temperatures in the nests reached 47.4° C. during the middle of the day.

The nighttime temperatures of the nestlings were taken between 5 and 44 minutes of the time the adults flushed from the rookery. Although at night the mean body temperature of the nestlings was 4° C. lower than the daytime mean temperature for shaded individuals, there was no trend toward depression of temperature with increasing length of exposure to the cool night air (air temperature 17.6° C.). None of the young herons shivered.

Behavior and temperature regulation. Young herons are somewhat more active than pelicans of comparable age and can crawl about in the nest to a limited degree. This offers the possibility of reaching whatever shade is available during the hottest parts of the day. Adult herons were in attendance at the nest both day and night. They flushed readily and remained several hundred yards away as long as we were near the rookery.

WESTERN GULLS

Western gulls nested at various points in Puerto Refugio, but all the nests were in exposed rocky situations. All but a few of the temperature measurements were made in a single rookery occupying the narrow, barren peninsula which separates the eastern and western anchorages. The nests were either completely exposed to the elements on the bare rock slopes, or partly protected in broken rocky areas on the east and west sides of the peninsula, and were scattered from high-

FIG. 4. Young California brown pelican at nest among boulders on Granite Island, Baja California, Mexico. In such situations downy individuals commonly retreated during the hottest part of the day into crevices, where shelter from the intense solar radiation was available.

tide line to an elevation of about 80 feet. Nesting was in an early stage, and none of the young was more than a week old (5½ to 8 inches long). Temperature conditions were similar to those described for the pelican and heron rookeries.

There was a statistically significant difference of almost 2° C. between the mean body temperatures of the nestlings exposed to the sun and of those in the shade (Fig. 5). Although the young gulls breathed rapidly through the open mouth when heated, no gular fluttering was observed. The mean nighttime temperature of the nestlings was less than 2½° C. lower than the mean temperature of the shaded young during the day. No shivering was observed.

Behavior and temperature regulation. Young gulls are downy when hatched and show more capacity for temperature regulation than either of the other species studied. In addition, their precocial development allows them to seek the shelter afforded by the rocks and crevices adjacent to most of the nests. The nests of the gulls often consisted only of a depression in the substratum and at best contained only fragments of dried sea weed. Adult gulls were much less attentive to their young than adults of either of the other species. They often left their young spontaneously for considerable periods of time.

Characteristically the young sought out any sheltered areas near their nests. They took advantage of the shelter afforded by rocks, crevices, a sea lion carcass, and pieces of debris. They even availed themselves of small patches of shade only large enough to shelter their heads.

DISCUSSION

Colonial marine birds nesting in exposed situations subject to environmental extremes offer uniquely favorable opportunities for analyzing the affects of physical environmental factors on critical aspects of vertebrate physiology and behavior. The data presented above allow comparison of young birds of three different levels of temperature regulatory capacity, which successfully meet

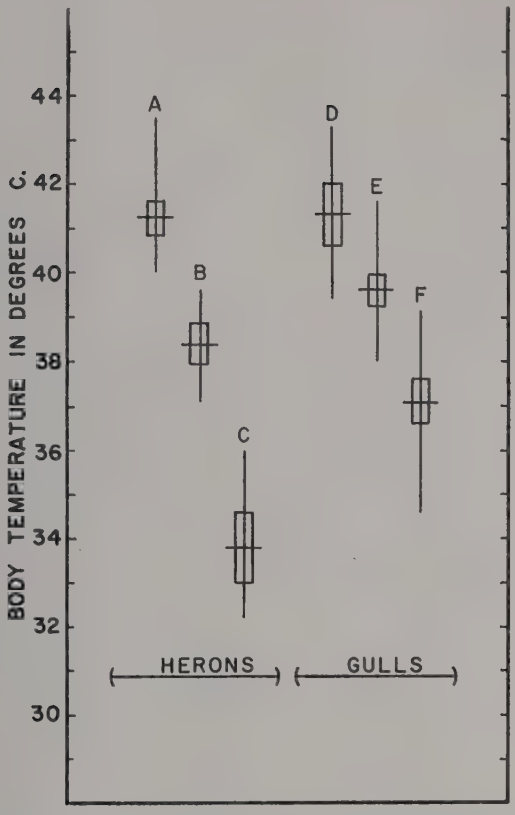

FIG. 5. Body temperatures of young great blue herons and young western gulls. The vertical lines indicate the range; the horizontal lines indicate the mean (M); and the rectangles indicate the interval $M + 2\sigma_M$ to $M - 2\sigma_M$. Units A-C: herons. Units D-F: gulls. A and D represent individuals exposed to direct sunlight during the middle of the day. B and E represent individuals shaded during the middle of the day. C and F represent individuals measured at night (2200-2400).

essentially identical environmental stresses.

For nesting birds of the species studied, the most critical factor of the physical environment in the Gulf of California is solar radiation. The clear skies and the low latitude make the problem of solar heating acute for many hours of each day during the nesting season. High air temperatures present a less critical problem, for this is an area of well developed sea breezes which moderate the air temperatures in the exposed rookeries.

The young of all three species were unable to prevent rises of several degrees C. in body temperature when exposed to direct solar radiation and only moderate air temperatures. A primary reason for this inability is that they, like all other birds and most mammals, do not possess sweat glands and so depend primarily on panting for evaporative cooling. This process involves the production of sufficient metabolic heat to make it inefficient from the standpoint of net heat dissipation. (Kendeigh 1944; Dawson 1954; Brody 1945: 278-279.)

Many birds (from personal observations, screech owls, *Otus asio;* nighthawks, *Chordeiles acutipennis;* mourning doves, *Zenaidura macroura;* cormorants, *Phalacrocorax* spp.; boobies, *Sula* spp.; and great blue herons, *Ardea herodias*) when heated, open the mouth and flutter the gular area rapidly. It is probable that this gular flutter increases the rate of evaporative cooling without causing a commensurate increase in metabolic heat production. As discussed elsewhere (Bartholomew, Dawson, and O'Neill 1953) this gular flutter reaches its fullest development in pelicans. It is of interest that this means of evaporative cooling was absent in newly hatched brown pelicans, as in young gulls of all ages, whereas it was well developed in newly hatched herons. Even with this mechanism for heat loss, nestling herons and downy pelicans showed marked elevations in body temperature when exposed to direct solar radiation.

The possession of down provides protection from solar heating during the day and from excessive heat loss during the night. Capacity for temperature regulation in nestlings of three species correlates with degree of development of down at time of hatching. However, even the downy nestling gulls possessed labile body temperatures, and it appears that temperature regulation in these birds consists not of the maintenance of body temperature at a constant level, but of its restriction to a range of approximately 8 degrees centigrade.

Under natural conditions the temperature regulation of the nestlings depends not only on their own physiological capacities, but to an important degree on the behavioral responses of their parents, which protect them from the direct impact of the environment. The degree of attentiveness of adults decreases as the homeothermy of their nestlings increases. On the other hand, behavioral patterns of nestlings, which tend to reduce heat stress, increase with their capacities for homeothermy, *i.e.,* the nestlings with the best muscular coordination were also the best temperature regulators. The gulls, the most advanced in development at time of hatching, had the greatest physiological capacity for temperature regulation and also were the most able to move about and seek shelter. The naked pelicans, the least advanced

at time of hatching, had the least physiological capacity for temperature regulation and were virtually unable to move about. The herons were intermediate in all respects with regard to temperature control. Except under extreme conditions, the youngest gulls are essentially independent of parental care for temperature regulation, whereas the youngest pelicans are totally dependent in this respect.

Not only are the naked nestling pelicans deficient in heat-dissipating capacity, but their heavy pigmentation favors the absorption of solar radiation. Despite the low air temperatures, individuals which had not been recently shaded acted like black bodies and were conspicuously hot to the touch. The naked young lack the subcutaneous pneumaticity which is so characteristic of the larger young and adults (Richardson 1939), and it is probable that this deficiency further increases their susceptibility to solar heating. Their survival despite all these inadequacies and the severity of the solar radiation is an indication of the effectiveness of the behavioral patterns of the adults.

The successful nesting of gulls, herons, and pelicans under similarly adverse conditions demonstrates clearly how terrestrial vertebrates can compensate for physiological inadequacies by relatively simple behavioral responses. In this manner organisms of very different physiological capacities can successfully exist in the same physical environment, even during the least resistant stage of their lives. Our observations emphasize the fact that students of distribution and ecology should employ extreme caution in attempting to explain differences in habitat selection or geographic distribution of closely related forms in terms of slight physiological differences.

Summary

Observations were made on temperature regulation in the young of two altricial birds (brown pelican and great blue heron) and one precocial bird (western gull), which nest in rookeries at the north end of Angel de la Guarda, a desert island located in the Gulf of California and characterized by intense solar radiation and extreme aridity. Overheating through exposure to direct insolation is a primary physiological problem faced by the young of all three species.

In the absence of parental care, body temperature in naked young brown pelicans is profoundly affected by both solar radiation and air temperatures (total diurnal range, 21.4 to 43.7° C.). Homeothermy increased with development of down; total diurnal range in large downy young was 37.8 to 41° C. Survival of the naked young during the day depends on their being shaded by the adults, which are very attentive.

Newly hatched great blue herons possessed somewhat greater temperature regulatory capacities than pelicans of comparable age. Although they showed elevated body temperatures when exposed to direct insolation, their body temperatures did not fall below 32.2° C. at night (daytime maximum, 43.5° C.). The adult herons were somewhat less attentive to their young than the adult pelicans.

Young gulls had a relatively great capacity for temperature regulation. Although essentially as sensitive to solar radiation as the newly hatched of the other two species, their temperatures in the absence of brooding did not fall below 34.6° C. at night (daytime maximum 43.3°). The adults were relatively inattentive to the young, and newly hatched gulls withstood direct solar radiation for as long as an hour without apparent ill effects.

The successful nesting of these three species in the same area at the same time despite their differences in capacity for temperature regulation emphasizes the importance of behavior as a supplement for physiological mechanisms in birds.

References

Bartholomew, G. A., Jr., and W. R. Dawson. 1954. Body temperature and water requirements in the mourning dove, *Zenaidura macroura marginella*. Ecology, **35**: 181-187.

Bartholomew, G. A., Jr., W. R. Dawson, and E. J. O'Neill. 1953. A field study of temperature regulation in young white pelicans, *Pelecanus erythrorhynchos*. Ecology, **34**: 554-560.

Brody, S. 1945. Bioenergetics and growth. New York: Reinhold Publ. Corp., xii + 1023 pp.

Dawson, W. R. 1954. Effects of heat on temperature regulation and water requirements of the brown and Abert towhees, *Pipilo fuscus senicula* and *Pipilo aberti dumeticolus*. Univ. Calif. Publ. Zool., in press.

Kendeigh, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English sparrow. Jour. Exp. Zool., **96**: 1-16.

Murphy, R. C. 1936. Oceanic birds of South America. New York: The American Museum of Natural History, xx + 1245 pp.

Richardson, F. 1939. Functional aspects of the pneumatic system of the California brown pelican. Condor, **41**: 13-17.

Simpson, S. 1910-1911. Observations on the body temperature of the domestic fowl (*Gallus gallus*) during incubation. Trans. Roy. Soc. Edinburgh, **47** (part III): 605-617.

Wetmore, A. 1921. A study of the body temperature of birds. Smithsonian Misc. Coll., **72**(12): 1-52.

JUNIPER-PINYON EAST OF THE CONTINENTAL DIVIDE, AS ANALYZED BY THE LINE-STRIP METHOD[1]

HOWARD E. WOODIN AND ALTON A. LINDSEY
Middlebury College, Middlebury, Vermont, and Department of Biological Sciences, Purdue University, Lafayette, Indiana

INTRODUCTION

A phytosociological study of the "pinyon-juniper association" in the eastern foothills of the Rocky Mountains was initiated in September, 1951 and ended in August, 1953. Two field trips totalling over 16,000 miles in four states were undertaken for the collection of data by the first-named author, one during the summer of 1952 and the other during the spring of 1953. Twenty-four representative stations were analyzed for comparing the community characteristics of pinyon-juniper stands throughout the eastern range of this type except in the extreme northern portion.

One of the primary objectives was the development of a sampling method sufficiently rapid for a broad reconnaissance study of a large region without sacrificing accuracy. This called for the statistical determination of adequacy of sampling. Another point considered important was obtaining reliable data on cover especially, because of its relation to erosion. These needs were met by combining into one sampling unit the line-interception principle plus a very long narrow quadrat. This unit is termed the "line-strip."

The main area studied extends from the Davis Mountains in Texas to the Colorado-Wyoming boundary and is bounded on the west by the continental divide. The latter forms a rather natural boundary for delimiting the scope of the problem to an area of manageable size. The area is mapped in Fig. 1, which also compares the boundary of this type as recognized by Shantz and Zon (1924) and the U. S. Forest Service (1949). Farther north, a single station was sampled in the Big Horn Mountains, Wyoming. Economically, the woodland is important mainly as grazing land; the timber has some importance as mine props, fuel, and fence posts. Of great importance is the cover it furnishes for wildlife, and the inhibiting effect it has upon erosion.

A literature review for the southwestern woodland type by Woodin (1953) is available in unpublished form.

CLIMATE

According to Pearson (1920), "In the pinyon-juniper type, we have high temperatures, high wind movement, and low relative humidity. The evaporation here is by far the highest recorded for any of the forest types. . . ."

Throughout the whole range of the type the winter precipitation is in the form of snow.

Data for characterizing the climate were gathered from the Annual Summaries of Climatological Data (U. S. Dept. Commerce 1951) for the states concerned. Twenty-three weather stations (Fig. 1) well within the pinyon-juniper areas were utilized, excluding stations that had not been in operation long enough (10 years) to have "departures from normal" recorded. The average figures for temperature and precipitation were calculated by adding and subtracting the departure from normal as the individual cases dictated. The weather stations thus selected are shown on the map (Fig. 1), and listed in its legend. For each of these 23 weather stations, the average temperature and total precipitation for each month, and the annual mean temperature and total precipitation, were tabulated.

Throughout most of the eastern range of the pinyon-juniper, about one-third of the yearly rainfall is received in July and August, one-sixth of the year. This is particularly true of the central portion of the range but in the more northerly (Colorado, Wyoming) and southerly (Texas) portions monthly rainfall exceeding 1½ in. comes as early as May or even April. The over-all climate is rather dry; the normal annual precipitation at the 23 weather stations ranges from 13 to 20 in. Their average annual rainfall is 16.1 inches. Approximately 10 to 12 in. supports no trees except widely spaced junipers.

The small amount of rainfall seldom penetrates below 30 centimeters and usually to about 15 (Emerson 1932). Soil moisture values may approach the permanent wilting percentage at a

[1] During the final year of the study, the first-named author held a National Science Foundation fellowship. The field work in the summer of 1952 was supported by a Purdue Research Foundation fellowship. For identification of plant specimens, we are indebted to Dr. C. V. Morton, Dr. D. B. Dunn, Dr. W. F. Winne, and Dr. C. W. T. Penland. Dr. F. L. Serviss confirmed rock identifications. Mrs. Beverly Woodin assisted in the field work and tabulations. The Committee for Biology of the Purdue Statistical Laboratory, and especially Dr. S. K. Suddarth of this Laboratory, were consulted in the methodology and statistical procedures. To these individuals and institutions the writers are very grateful.

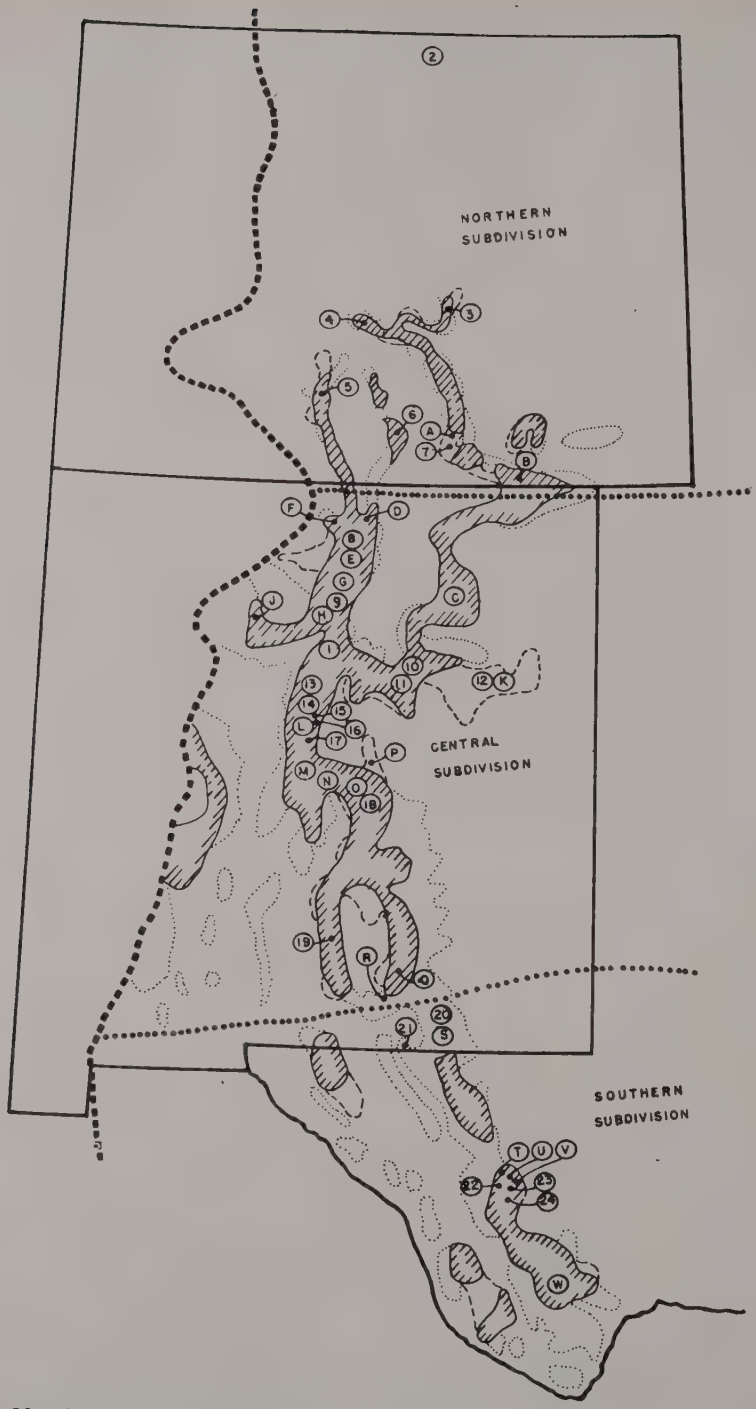

FIG. 1. Map showing limits of the Shantz-Zon "pinyon-juniper" association (light dotted lines) and limits of the U. S. Forest Service "conifer woodland" type (dashed lines). The hatched boundaries include areas common to both. Locations of vegetational sampling stations are numbered. Letters indicate Weather Bureau stations as follows—*Colorado:* A, Walsenburg; B, Trinidad; *New Mexico:* C, Aurora; D, Cerro; El Rito; F, Terra Amarillo; G, Espanola; H, Bandelier; I, Regina; J, Santa Fe; K, Conchas Dam; L, Tajique; M, Mountainair; N, Progresso; O, Corona; P, Duran; Q, Elk; R. Mayhill Ranger Station; S, Carlsbad Cavern; *Texas:* T, Mt. Locke; U, Ft. Davis; V, Alpine; W, Marathon. Three general climatic and vegetational subdivisions are separated by heavy dotted lines.

depth of 6 in. or more during May and June (Pearson 1920). The rainfall during July, August, and September follows a daily pattern of small local showers in the pinyon-juniper country. In the southern portion, the moisture-laden air is carried northward from the Gulf of Mexico during the summer months into a region of low pressure developed over the hot desert lands of the Southwest. In the winter, this region of low pressure is replaced by a high pressure area which leads to northerly and easterly winds from the relatively dry interior of the continent where an even higher pressure area is developed. The summer low moves in slowly from the oceanic regions to the southeast during the spring months and as it moves over the land masses toward the northwest it brings rain with it. Therefore, the more inland regions have their rainy season progressively later as the low pressure area works westward. Precipitation in the type generally increases with altitude, while the evaporation rate decreases because of lower temperature.

Great daily and seasonal variations in temperature occur. "The daily range is greatest in the lower altitudes . . . about 50° F. in the pinyon-juniper . . ." (Pearson 1920). The range of monthly mean temperatures taken from the climatological data shows a mean at Carlsbad Caverns during July of 78.4° F. and a January mean of 45.0° F., while Cerro, New Mexico reports a July mean of 66.4° F. and a January mean of 20.8° F. Livingston and Shreve (1921) set the annual mean for this type from 40° to 70° F. whereas our analysis of more long-term climatological data indicates a range of 43° to 54° F. for the stations selected.

In central and southern New Mexico, due to comparative cloudiness during July and August, the hottest portion of the year on the basis of means, the hottest individual days fall in June. For example, in the vicinity of Carlsbad, New Mexico, the highest maxima come in June, reaching occasionally to 112° F.

The frostless period in pinyon-juniper country ranges from 91 to 205 days, according to the records of the selected weather stations.

The decision for dividing the area studied into three subdivisions (Fig. 1) is based primarily upon precipitation periods, since rainfall is considered to be more important than temperature in determining the vegetational differences among the subdivisions. Figure 2 gives hythergraphs (Smith 1940) for the three. The earliest month having heavy precipitation varies considerably. In

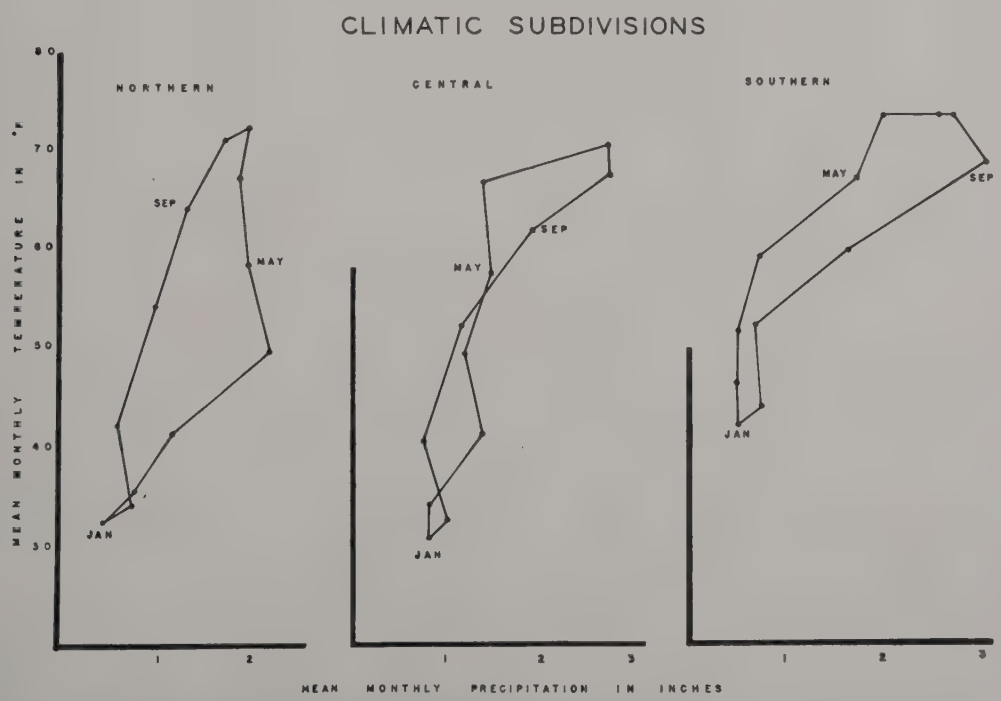

FIG. 2. Mean monthly temperature plotted against average of the normal monthly precipitation for the three climatic subdivisions of the juniper-pinyon type east of the Rockies. Each point is an average of the monthly figures from the several weather stations within one subdivision.

the northern subdivision this month is April, which has one inch more rainfall than March. A similar increase does not take place until July in the central subdivision, and May in the southern subdivision. This marked difference in the time of onset of the rainy season has dictated the position of the boundaries between the three subdivisions.

The northern climatic subdivision is bounded on the south by the Colorado-New Mexico border and extends north through Colorado, but its northern boundary is impossible to determine due to the lack of weather stations in juniper vegetation in Wyoming. Therefore, sample station 1 (Big Horn Mountains, Wyoming) has not been included in the climatic correlations. The northern subdivision is affected by the prevailing westerlies and the precipitation there is largely a result of the cyclonic storms from the west. Here the precipitation is spread over a longer period, April through August.

The central subdivision is bounded on the north by the Colorado-New Mexico border and on the south by a line connecting Las Cruces and Artesia, New Mexico. The latter line forms the northern boundary of the southern subdivision, which, as far as this study is concerned, extends southward to the Rio Grande. How far this subdivision might extend into Mexico is not known.

Individual Sample Stations

Rather than utilize all topographic situations indiscriminately, which would lead to unnecessary complexity, stations were restricted to two topographic situations, as explained later under Methods. All slopes mentioned face toward the east. Detailed physical descriptions for all 24 stations are given by Woodin (1953); the present paper merely lists the dates of study, locations, altitudes, and slopes, except for the one station considered most representative of each of the three climatic subdivisions. These three stations are 6, 10, and 23. The individual stations are listed in order from north to south regardless of when they were studied.

Station 1. August 12-14, 1952; 10 mi. east of Tensleep, Wyoming; 5600 ft.; 18 per cent slope.

Station 2. August 5-7, 1952; 16 mi. north of Fort Collins, Colorado, east of Rt. 287; 6000 ft.; 17 per cent. Beidleman (1953) gives a popular account of this stand which is now being destroyed by quarrying.

Station 3. July 28-39, 1952; 22 mi. southwest of Colorado Springs, Colorado, south of Rt. 115; 6300 ft.; level.

Station 4. May 11-12, 1953; 7 mi. east of Salida, Colorado, on Rt. 50; 6950 ft.; level.

Station 5. May 9-10, 1953; 6 mi. west of Suguache, Colorado, north of Rt. 114; 7800 ft.; level.

Station 6. This station was located at an elevation of 8400 ft. approximately 1.5 miles east of Fort Garland, Costilla County, Colorado. It lies south of Route 160 on a dirt road leading to the "Trinchera Ranch" and thence one-fourth mile north.

The station site was the level top of a long, flat ridge extending south from higher mountains in the vicinity of Blanca Peak. The ridge was one of several similar ridges paralleling each other and each covered with pinyon-juniper while the valleys between had sagebrush communities. The site was classed as level (0-5 per cent). The sloping sides of the ridge carried woodland species but were not studied since they were not extensive enough to be worthy of a separate station.

The soil was very coarse with no bedrock exposed even on the steep sides. The heterogeneity of the soil was evidence that it had not been produced *in situ*. The soil of the valleys between the tongues of higher ground was considerably finer textured. The pinyon-juniper community avoids the more poorly drained condition of these valleys. The area is being grazed at the present time, as are all the woodland areas throughout this general region. There was evidence, at the time of study, that there was a crop of pinyon seed during 1952, but, while empty cones were plentiful, there were no full seeds. Both pinyon and Rocky Mountain juniper were represented by young seedlings of one or two season's growth. The area was visited May 6 and 7, 1953.

Station 7. July 21-22, 1952; 2 mi. west of Walsenburg, Colorado, on top of a mesa 1 mi. south of Rt. 160; 6400 ft.; level.

Station 8. May 2-3, 1953; 9 mi. north of Ojo Caliente, New Mexico, northwest of Rt. 285; 7100 ft.; level.

Station 9. July 15-16, 1952; Santa Fe National Forest a few miles north of Santa Fe, New Mexico; 7500 ft.; level.

Station 10. Located on the west side of Route 84 about 22 miles south of Las Vegas, New Mexico, in San Miguel County, Sta. 10 was studied April 13-14, 1953. The site was the side of a large hinged uplift which is one of a series of similar uplifts with north strikes and east dips. The general slope was 28 per cent and the elevation of the center of the study area was 5600 ft.

The top layer of bedrock was limestone and at spots toward the upper portion of the slope bare rock was exposed where trees were rooted in joints of the bare rock.

The soil was residual and fine-textured, having

weathered out of the top limestone layer, and tested basic. Toward the toe of the slope, talus was exposed but the large broken pieces did not form any great portion of the surface. Litter was present everywhere but was naturally deeper beneath the trees where it may have reached 2 in. before grading into the humus layer.

Erosion had formed some channels which traverse the slope parallel to the dip of the uplift.

The area was fenced but no cattle were seen and there was no indication that there had been grazing within the last year. Some of the pinyons had been cut but not within the last few years.

Station 11. May 13-14, 1953; 30 mi. south of Las Vegas, New Mexico; 5200 ft.; level.

Station 12. April 10-11, 1953; 47 mi. northwest of Tucumcari, New Mexico, 3 mi. west of Conchas Dam on Rt. 129; 4600 ft.; level.

Station 13. June 18-20, 1952; South Cibola National Forest about 10 mi. east of Albuquerque, New Mexico; 6250 ft.; level.

Station 14. June 20-21, 1952; adjacent to Sta. 13; 6300 ft.; 15-30 per cent slope.

Station 15. April 18-19, 1953; east of Albuquerque on Rt. 10, 3 mi. south of Rt. 66; 6480 ft.; level.

Station 16. April 21-22, 1953; 3 mi. south of Sta. 15; 6800 ft.; level.

Station 17. April 24-25, 1953; 6 mi. south of Sta. 15; 7100 ft.; level.

Station 18. June 23-24, 1952; 17 mi. south of Corona, New Mexico, west of Rt. 54; 6800 ft.; level.

Station 19. June 27-28, 1952; halfway between Alamogordo and Cloudcroft, New Mexico, on Rt. 83; 6000 ft.; 27 per cent slope.

Station 20. July 2-3, 1952; 2 mi. east of Pine Springs, New Mexico; 5500 ft.; level.

Station 21. July 3-4, 1952; Carlsbad Caverns National Park, New Mexico; 4300 ft.; 15 per cent slope.

Station 22. July 5-6, 1952; Indian Hill in the Davis Mts., Texas; 6000 ft.; level.

Station 23. In the extreme western portion of Texas, in the Davis Mountains, Sta. 23 was studied July 6 and 7, 1952. The mountains are of volcanic origin and the rock samples collected from all three stations located in this region were tuff or some type of magmatic rock.

This station was located near the Rockpile Park area and was a level (0-5 per cent) area at about 6150 ft. elevation. Throughout the area the vegetation had been browsed and grazed by both cattle and wild deer (principally the mule deer, *Odocoileus hemionus*). Erosion was of minor importance. There was a definite layer of topsoil, thin in places, but enough to support a well-developed lower stratum of vegetation.

The vegetation appeared unusually luxuriant. The component species reflect the southerly aspect of the woodland type. The pinyon was *P. cembroides.* Also, *J. pachyphloea, J. texensis, Quercus grisea* and *Q. emoryi* were prominent. This represents the *Quercus-Juniperus* association of Weaver and Clements (1938).

Station 24. July 7-8, 1952; Elbow Canyon in the Davis Mountains, Texas; 6300 ft.; 17 per cent slope.

Methods

Sample stations at the various latitudinal positions within the pinyon-juniper type (Fig. 1) were located as nearly as possible in a typical stand for that particular latitude rather than in the ecotones above or below. This point was determined by traversing the stand, preferably altitudinally, and then returning to the observed midpoint. This median position usually carries some mixture of both pinyons and junipers.

To make significant comparisons possible over the wide geographic range, certain site requirements were prescribed, so that all the data represent just two types of terrain as regards slope and exposure. Only level areas of 0-5 per cent slope and east-facing slopes of 15-30 per cent were used; borderline cases were measured by Abney level. Three-fourths of the stations sampled were on level land, the remainder in the moderate slope class, and all of the stations supported an upper stratum of trees. Many slopes where pinyon-juniper stands occur are over 30 per cent, *e.g.,* the steep talus slopes of mesa and canyon walls. Gentle undulations in the terrain of an area did not preclude its use as a level site providing the general over-all slope did not exceed 5 per cent. East-facing slopes were used if they faced between northeast and southeast.

At each station, collections were made of all unknown plants, and samples of bedrock and soil were taken. Extensive notes and numerous photographs were taken describing and showing the physiography and condition of the stand. The altitude of each station was recorded from a pocket altimeter which was checked as often as possible with known altitudes and bench-marks.

Due to the fact that the basis of this study is a general reconnaissance of a very large area, a method of measurement of the communities was needed which was economical of time while not sacrificing accuracy. Since the trees are widely spaced and large open areas sometimes occur in stands, laying out square or circular quadrats of sufficient size and number would take so much

time that few stands could be examined. Furthermore it is very time-consuming to determine cover accurately by quadrats, regardless of shape; the authors are in agreement with Bauer (1943), Penfound (1945), Buell and Cantlon (1950), and Merkle (1952) that cover is the most expressive of all the phytosociological attributes.

The line-interception method proposed by Canfield (1941) is an excellent way of measuring cover only. This method, first used by Canfield on grass ranges, has been investigated by Bauer (1943) who concluded from both field and artificial population analyses that it is highly satisfactory for rapid and accurate determination of cover. Although Bauer recommended the method for density and frequency determinations also, it is poorly adapted for these because larger-crowned species are more likely to intercept the line. This introduces marked statistical bias into frequency and density data in favor of such species. Buell and Cantlon (1950) were aware of this weakness when they used the line-interception method in studying a tree community in the New Jersey pine barrens, in comparison with the quadrat method.

By combining quadrat and line-interception methods the advantages of both can be utilized without incurring any marked disadvantages.[2] It has been decided to call this combination the "line-strip" method. Cover data are gathered from the "line" whereas density, abundance and frequency are derived from the areal "strip" (Fig. 3). The term "transect" has not been used since it preferably refers to a line or belt traversing an entire community or transition zone while the line-strip is utilized not singly at a station but in numbers. The line-strip consists of a surveyed line placed at random within a stand, bisecting an unsurveyed strip; the length of both and the width of the strip depend upon the type of vegetation or the particular stratum being studied. The strip has square ends. The boundaries of the strip are estimated, except when trunks are so near a boundary as to be in doubt. The strip component, then, is a quadrat which is very long in relation to its width, and easy to establish considering its area.

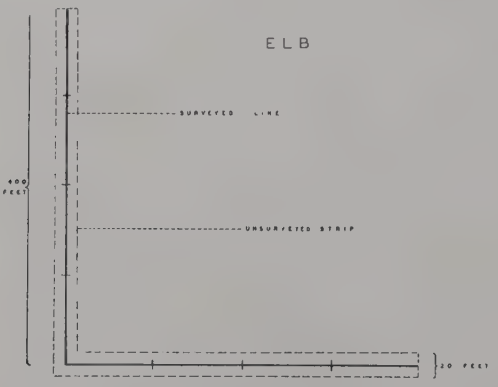

FIG. 3. Diagram of an 800-foot line laid out by a steel tape (solid line) and the 20 foot areal strip bounded by a dashed line. A line-strip bent at right angles is termed an "elb."

[2] In personal conversation in December 1951 between Buell and Lindsey, it was learned that both had independently arrived at the basic principle of the sampling unit here termed the straight line-strip.

In the pinyon-juniper association, an 800 ft. line was utilized bisecting a 20 ft. wide strip. There was seldom any doubt in this sparse community whether or not a tree-center fell within the strip. The term "elb," which is short, expressive, and neither an archaic nor current word in any language so far as is known, was coined to apply to the line-strip of special form used in this study. Although other workers have used only straight lines, the bent form was adopted for pinyon-juniper vegetation because one or more of the straight lines at a station, when placed at random, might fall largely within the linear influence of gullies, ridges, slope bases, rock joints and crevices, or particular bedrock strata. The 800 ft. line-strip was bent in the center so that it consisted of two 400 ft. halves forming a right angle at their junction point. This length appeared to be sufficient to take into consideration relatively minor irregularities in the stand or in the topography. It appears that the length of line as well as the number of lines needed for adequate sampling is dictated by the spacing of the vegetational units and the heterogeneity of the stand. The advantage of great length is that, according to Dr. J. H. B. Kemperman and Dr. S. K. Suddarth, the results can be treated statistically as if the stand were assembled randomly even if it might not be actually so. The number of lines was determined on the first field trip by determining the standard error of the mean line-interception per elb of the most prevalent species at each station. Later, during the spring trip of 1953, to eliminate mathematical calculations in the field and to facilitate computations in the laboratory later, a constant number (7) of elbs were laid out at each station. This number was arrived at by studying the results of the work of the previous summer, and was subsequently found to be sufficient to yield acceptably low standard errors for the dominant species. By dividing the work, two operators can survey, and record data from, an 800 ft. line-strip in from 1½ to 2 hours depending upon the density of the stand.

Once the area to be studied had been deter-

mined, preferably 80-100 acres, a mimeographed random numbers table was used in the field to determine, by coordinates on a rough map drawn to scale on graph paper, the position of elb corners within the stand. The compass bearing of the first elb-half was determined by using three consecutive random numbers, rejecting combinations over 360. The second elb-half was directed right or left if the next random number was even or odd respectively. All seven elbs were then mapped before laying out the first one, and numbered to allow a convenient circuit through the tract. Since the object was merely to locate sampling units randomly, tedious accurate surveying was pointless, and they were placed by pacing on a compass bearing.

After reaching the position of an elb, work on it was begun by laying a 200 ft. steel surveyor's tape marked off in feet and tenths along the previously mapped line, and securing its ends by 6 in. nails. A steel pocket tape was used for the few trees with trunk centers too close to the ten-foot limit to be judged inside or outside with certainty.

In order to obtain a measure of cover, crown interceptions were recorded. Since the branches providing cover from either pinyons or the various junipers were seldom more than 10 ft above the ground level, an imaginary plumb line was dropped from the two places where the crown edge intersected the line and the figures recorded. Stem diameters were estimated to the nearest inch. Only those trees within the strip which had a stem diameter (at one foot height) of at least 4 in. or its equivalent were used for abundance, basal area, or density computations, but all plants more than 3 ft. tall which intercepted the line were recorded for cover. The latter height was selected to separate the trees and tall shrubs of the upper stratum from the lower stratum as two distinct analytical groups. Trees were not measured for diameter at the customary breast height (4.5 ft.) because low branching characterizes this woodland type. The one foot height usually fell below the branching and yet was above the low butt-swell. *Juniperus monosperma* presented a problem in basal area since it frequently branches at or below the ground surface. Diameters of the various stems were taken at the 1 ft. level and averaged in the field. For each crown, the number of stems and the average diameter were recorded. Later the average diameter was converted by a table to basal area in square feet and this figure multiplied by the number of branches. Only those individuals (crowns) having a total stem basal area figure equivalent to that of a single 4 in. stem or larger were used for per cent total abundance, basal area, or density.

The mimeographed record sheet for upper stratum species has columns for species name, and "a," "b," "b-a," "c," and stem diameter figures. The meaning of the letter symbols follows:

a represents the first intersection of any one unit on the line.

b represents the last intersection of any one unit on the line.

b-a represents the interception distance of any one unit in feet. The sum of all interceptions for a given species for one line-strip is termed the "line-cover" for that line-strip.

c column is used for recording, by its initial or a check mark, the presence of the trunk centers of all trees within the 20-ft. strip, whether they furnish line cover or not. This is the basis for determining density.

During the first field trip, in the summer of 1952, data for the lower stratum consisting of grasses, forbs and shrubs less than 3 ft. tall were recorded from the last 50 ft. of each end of the elb.

The mean crown diameter of a given species in a stand may be compared with that in other stands as one criterion of site quality. Mean crown diameter (D) may be calculated, without any measurements or estimates of this dimension in the field, by the following formula:

$$D = 2\sqrt{\frac{(C)\ 43560}{\pi d}}$$

where C is the per cent ground cover obtained from the line-cover data, and d is density per acre obtained from strip data.

Results

The results of the field and laboratory work may best be summarized with the use of tables and illustrations.

That the use of line-strips proved valuable is due in part to the fact that the central line provides a more accurate and easier method of determining cover than the quadrat or belt transect. The percentage of the total line length intercepted by a species at a station is a reliable estimate of the percentage cover per acre contributed by that species at the station. This presents a simple and accurate method of determining such attributes as per cent ground cover, per cent vegetation cover, and square ft. per acre cover, which are given in Table I. This table deals with the upper stratum only. The lower stratum was studied only at the 14 stations visited in the summer of 1952, and these results are fully tabulated in Woodin (1953).

Per cent total abundance of a species was obtained by dividing the total number of individuals of all upper-stratum species into the number of

TABLE I. *Phytosociological attributes of trees and tall shrubs. Cover figures are based on all plants exceeding 3 ft. in height. Other values are based on trees with stem diameter exceeding 4 in. at the 1 ft. height, and on shrubs exceeding 3 ft. in height*

Station	Species	% Total abund.	Basal area in sq. ft./ Acre	Cover			Density per acre
				% veg.	% ground	sq. ft. per acre	
1	*Juniperus monosperma* (Englem.) Sarg.	95.7	87.02	97.0	19.4	8,450.6	209.9
	Rhus trilobata (Nutt.) Munz	4.3	—	3.0	.6	261.4	14.3
2	*Pinus edulis* Englem.	65.1	20.35	83.9	35.4	15,420.2	130.0
	Cercocarpus m. montanus Raf.	27.4	—	11.8	5.0	3,178.0	162.9
	Juniperus scopulorum Sarg.	7.4	6.46	4.3	1.8	784.0	33.9
3	*P. edulis*	73.3	50.25	80.1	32.2	14,026.3	191.8
	J. monosperma	26.7	24.85	19.9	8.0	3,484.8	102.1
4	*P. edulis*	69.1	37.40	80.6	14.9	6,494.8	115.9
	Opuntia acanthocarpa Engelm. & Bigel.	5.8	—	.9	.2	78.4	
	Ribes leptanthum Gray	7.4	—	5.1	.9	409.6	
	J. scopulorum	5.3	3.25	6.1	1.1	487.9	6.6
	R. trilobata	12.6	—	7.3	1.4	592.4	
5	*P. edulis*	62.4	54.00	77.4	13.9	6,037.4	106.2
	Physocarpus intermedius (Rybd.) Schneid.	15.6	—	6.7	1.2	522.7	
	Chrysothamnus spp.	16.5	—	10.8	1.9	840.7	
	J. scopulorum	5.5	4.32	5.0	9.0	392.0	6.2
6	*P. edulis*	70.1	89.66	78.8	25.2	10,994.5	134.9
	J. scopulorum	10.1	11.32	12.8	4.4	1,907.9	15.9
	Artemisia tridentata Nutt.	19.9	—	8.4	2.9	1,258.9	
7	*J. monosperma*	62.7	62.72	57.1	13.3	5,793.5	109.3
	P. edulis	37.3	19.51	42.9	10.0	4,356.0	51.3
8	*P. edulis*	61.4	47.56	71.8	17.3	7,518.5	127.2
	J. monosperma	18.7	16.15	20.4	4.9	2,138.8	34.2
	Artemisia tridentata	16.3	—	6.2	1.5	635.9	
	Chrysothamnus spp.	3.6	—	1.6	.4	161.2	
9	*P. edulis*	53.6	26.49	58.3	12.0	5,227.2	121.0
	J. monosperma	46.4	31.51	41.7	8.6	3,746.2	125.9
10	*P. edulis*	29.6	8.87	31.6	3.9	1,698.8	33.8
	J. monosperma	63.4	21.12	64.8	8.0	3,484.8	62.2
	Quercus undulata Torr.	5.6	—	3.1	.9	165.5	
	Q. emoryi Torr.	1.3	—	.6	.1	34.	
11	*P. edulis*	12.2	3.27	14.2	1.61	701.3	12.4
	J. monosperma	87.8	36.75	85.8	9.8	4,264.5	69.6
12	*P. edulis*	15.5	1.58	15.3	1.8	797.1	9.3
	J. monosperma	65.9	27.94	78.0	9.3	4,055.4	50.9
	Rhus microphylla Engelm.	3.0	—	.8	.1	43.6	
	R. trilobata	13.4	—	5.6	.7	291.8	
	O. acanthocarpa	2.1	—	.2	.0	13.1	
13	*P. edulis*	16.8	6.40	11.8	3.2	1,393.9	50.9
	J. monosperma	79.5	54.26	85.7	23.0	10,018.8	158.1
	J. scopulorum	1.6	—	1.7	.5	217.8	3.0
	C. mentanus Raf. var. *paucidentatus* (S. Wats.) F. L. Martin	1.0	—	.4	.1	43.6	9.5
	Q. undulata	1.0	—	.4	.1	43.6	5.0
14	*J. monosperma*	77.9	51.23	86.0	24.0	10,454.4	218.4
	P. edulis	14.9	13.77	10.0	2.8	1,219.7	67.9
	Q. undulata	6.7	—	1.1	1.1	479.2	33.5
	R. trilobata	.5	—	—	—	—	15.1
15	*P. edulis*	39.5	18.50	37.8	12.9	5,614.9	109.7
	J. monosperma	53.1	46.98	57.9	19.7	8,598.7	122.1
	Q. undulata	4.4	—	2.8	.9	409.5	
	R. trilobata	1.3	—	.5	.2	78.4	
	Q. emoryi	1.0	—	.7	.2	104.5	
	C. m. montanus	.8	—	.3	.1	39.2	

Station	Species	% Total abund.	Basal area in sq. ft./ Acre	Cover			Density per acre
				% veg.	% ground	sq. ft. per acre	
16	*P. edulis*	25.3	11.93	29.2	5.8	2,548.3	33.1
	J. monosperma	51.1	18.03	45.8	9.2	3,994.5	62.2
	J. scopulorum	20.4	10.50	23.8	4.8	2,082.2	26.8
	Quercus sp.	3.3	—	1.2	.2	104.5	
17	*P. edulis*	31.9	17.41	37.3	8.7	3,781.0	53.7
	J. scopulorum	43.6	16.19	39.2	9.1	3,977.0	66.5
	P. ponderosa Dougl.	5.6	12.32	10.0	2.3	1,019.3	11.3
	J. monosperma	4.6	1.16	4.2	.9	422.5	5.1
	J. pachyphloea Torr.	2.8	1.64	4.7	1.1	479.2	3.9
	Quercus sp.	11.6	—	4.5	1.1	457.4	
18	*J. monosperma*	67.0	11.69	52.2	8.4	3,659.0	97.5
	P. edulis	24.3	3.74	24.8	4.0	1,742.4	82.7
	Q. undulata	18.5	—	9.9	1.6	696.9	117.8
	Berberis haematocarpa Wooton	6.9	—	6.2	1.0	435.6	27.8
	R. trilobata	9.5	—	4.3	.7	304.9	71.0
	Atriplex canescens (Pursh) Nutt.	2.6	—	2.5	.4	174.2	11.1
19	*J. monosperma*	22.0	11.11	47.8	6.6	2,874.9	372.8
	R. trilobata	30.0	—	15.9	2.2	958.3	205.8
	P. edulis	14.0	5.86	15.2	2.1	914.8	48.0
	C. m. paucidentatus	16.0	—	8.0	1.1	479.2	123.6
	Q. undulata	8.0	—	6.5	1.6	392.0	34.9
	Larrea tridentata (DC.) Coville	2.7	—	2.2	.3	130.7	11.2
	Ceanothus greggii Gray	4.0	—	2.2	.3	130.7	26.5
	Koeberlinia sp.	2.0	—	1.4	.2	87.1	8.0
	Fouquieria splendens Engelm.	.7	—	.7	.1	43.6	4.3
	Rhus microphylla	.7	—	—	—	—	8.2
20	*R. trilobata*	20.0	—	23.2	2.3	1,001.9	61.4
	C. greggii	22.4	—	19.2	1.9	827.6	92.5
	J. monosperma	15.9	1.43	18.2	1.8	748.1	51.4
	Quercus pungens Liebm.	15.4	—	15.1	1.5	653.4	55.7
	Microrhamnus ericoides Gray	11.4	—	10.1	1.0	435.6	44.0
	C. m. paucidentatus	10.0	—	8.0	.8	348.5	44.5
	Rhus glabra L.	3.0	—	4.0	.4	174.2	8.7
	Quercus hevardii Rydb.	2.0	—	2.0	.2	87.1	6.7
21	*J. monosperma*	99.1	23.89	97.6	20.5	8,929.8	224.5
	Caesalpinia sp.	.9	—	2.4	.5	217.8	7.8
22	*Quercus grisea* Liebm.	48.8	11.12	48.9	15.0	6,534.0	114.6
	Pinus cembroides Zucc.	31.8	7.41	30.0	9.2	4,007.5	77.2
	Q. emoryi	16.1	3.33	17.6	5.4	2,352.2	33.7
	J. pachyphloea	2.4	—	2.6	.8	348.5	4.6
	Juniperus texensis Van Melle	.9	—	1.0	.3	130.7	2.4
23	*J. pachyphloea*	61.2	15.47	59.1	19.4	8,450.6	116.7
	P. cembroides	28.1	3.47	29.0	9.5	4,138.2	50.4
	Q. emoryi	5.6	—	7.6	2.5	1,089.0	7.5
	J. texensis	5.1	—	4.3	1.4	609.8	11.5
24	*J. pachyphloea*	63.8	13.51	64.0	13.0	5,662.0	98.0
	P. cembroides	17.7	2.12	17.7	3.6	1,568.2	27.2
	J. texensis	10.6	2.26	9.9	2.0	871.2	11.5
	Q. emoryi	7.8	—	8.4	1.7	740.5	7.5

individuals of one species times 100. Density per acre is found from the field record sheets by reducing or expanding the number of plants having stem centers within the strips.

Table II serves for judging the adequacy of sampling within the stations. It shows for each station the mean line-cover per elb, and its standard error. Line-cover is the sum of all interceptions for a given species for one line-strip. An interception is the interval on the line covered by an individual crown. (The plus or minus figure shows that there is a 67 per cent probability that the true value for the mean lies within the range given. This is the probability for one standard error.) Sampling for the particular species is considered adequate if its standard error does not exceed 20 per cent of the mean. The per cent error is generally much less than this for the im-

portant species of a stand. For those species furnishing little cover in the stand, small per cent errors cannot be attained with a practicable number of elbs. Since it is low coverage which best indicates lack of phytosociological importance, use of enough elbs to yield less than 20 per cent error for these species would be unjustifiable in a survey study of wide geographical scope.

The average station per cent error for the *Pinus edulis* cover was 12.5; this value for *Juniperus monosperma* was 9.9 per cent. Thus, results of the sampling procedure proved quite acceptable

TABLE II. *Mean line-cover averaged at each station, and standard error. Based on all plants exceeding 3 ft. in height*

Station	Species	Mean line-cover in feet	Standard error	% Error
1	*Juniperus monosperma*	155.2	±13.9	9.0
	Rhus trilobata	4.6	± 2.2	47.8
2	*Pinus edulis*	283.5	±15.2	5.4
	J. scopulorum	14.1	± 3.0	21.3
	Cercocarpus m. montanus	40.1	± 9.0	22.4
3	*P. edulis*	257.5	±18.1	7.0
	J. monosperma	64.0	± 6.8	10.6
4	*P. edulis*	119.2	± 8.9	7.4
	Opuntia acanthocarpa	1.4	± 1.8	29.8
	Ribes leptanthum	7.5	± 2.0	26.0
	J. scopulorum	9.0	± 1.8	20.5
	R. trilobata	10.9	± 2.4	21.7
5	*P. edulis*	110.9	± 4.9	4.4
	Physocarpus intermedius	9.6	± 2.3	23.6
	Chrysothamnus sp.	15.5	± 3.5	22.3
	J. scopulorum	7.2	± 2.9	41.1
6	*P. edulis*	216.2	±10.2	4.7
	J. scopulorum	7.8	± 7.8	22.3
	Artemisia tridentata	23.1	± 3.5	15.1
7	*P. edulis*	79.8	± 8.5	10.7
	J. monosperma	106.2	± 8.8	8.3
8	*P. edulis*	138.1	± 6.2	4.5
	J. monosperma	39.3	± 5.2	13.1
	A. tridentata	11.9	± .8	6.4
	Chrysothamnus sp.	2.9	± .9	31.2
9	*P. edulis*	96.0	± 9.6	10.0
	J. monosperma	68.8	± 6.2	9.0
10	*P. edulis*	31.2	± 4.7	15.0
	J. monosperma	64.1	± 6.2	9.7
	Quercus undulata	3.0	± 1.2	38.9
	Q. emoryi	.6	± .4	64.6
11	*P. edulis*	12.9	± 2.8	21.7
	J. monosperma	78.3	± 5.1	6.5
12	*P. edulis*	14.7	± 2.4	16.1
	J. monosperma	74.5	± 8.6	11.5
	Rhus microphylla	.8	± .5	65.3
	R. trilobata	5.4	± 1.8	33.7
	Opuntia acanthocarpa	.2	± .2	100.0
13	*P. edulis*	25.5	± 5.9	23.1
	J. monosperma	184.2	±15.2	8.3
	J. scopulorum	3.7	± 2.8	75.7
	Cercocarpus m. paucidentatus	.5	± .5	100.0
	Q. undulata	1.0	± .7	70.0
14	*J. monosperma*	192.0	± 8.1	4.2
	Q. undulata	9.1	± 3.8	41.8
	P. edulis	22.4	± 5.1	22.8
	R. trilobata	.1	± .1	100.0
15	*P. edulis*	103.1	± 8.3	8.0
	J. monosperma	157.9	±10.8	6.9
	Q. undulata	7.6	± 1.8	24.1
	R. trilobata	1.4	± .6	40.8
	Quercus emoryi	1.9	± .7	35.5
	C. m. montanus	.7	± .5	69.0
16	*P. edulis*	46.8	± 6.8	14.4
	J. monosperma	73.3	± 2.7	3.7
	J. scopulorum	38.2	± 5.3	13.9
	Quercus sp.	1.9	± .8	45.2
17	*P. edulis*	69.4	± 6.6	9.5
	J. scopulorum	73.1	± 6.4	8.8
	Pinus ponderosa	20.2	± 2.6	13.1
	J. monosperma	7.7	± 2.3	30.3
	J. pachyphloea	8.8	± 2.4	27.6
	Quercus sp.	8.4	± 1.4	16.6
18	*P. edulis*	32.2	± 5.1	15.8
	J. monosperma	67.0	± 3.5	5.2
	R. trilobata	5.8	± .6	10.3
	Q. undulata	13.1	± 3.0	22.9
	Berberis haematocarpa	7.6	± 1.5	19.7
	Atriplex canescens	2.8	± 1.2	42.9
19	*J. monosperma*	53.0	± 3.7	6.9
	Fouquieria splendens	.4	± .4	100.0
	R. trilobata	17.9	± 3.1	17.3
	C. m paucidentatus	8.5	± 2.2	25.9
	Q. undulata	7.5	± 3.0	40.0
	P. edulis	16.7	± 4.6	27.5
	Koeberlinia spp.	1.8	± .8	44.4
	Ceanothus greggii	2.5	± 1.2	48.0
	Larrea tridentata	2.6	± 1.6	61.5
	Rhus microphylla	.2	± .2	100.0
20	*J. monosperma*	14.1	± 2.4	17.0
	Rhus glabra	2.9	± 1.0	32.8
	C. greggii	15.5	± 1.9	12.3
	R. trilobata	18.5	± 2.7	14.6
	Quercus pungens	12.2	± 1.7	13.9
	Microrhamnus ericoides	8.5	± 1.4	16.5
	Quercus hevardii	1.7	± .7	41.2
	C. m. paucidentatus	6.4	± 2.0	31.3
21	*J. monosperma*	164.2	±15.0	9.1
	Caesalpinia sp.	3.6	± 3.6	100.0
22	*Quercus grisea*	119.6	±10.5	8.8
	Q. emoryi	43.3	± 7.9	18.2
	Juniperus texensis	2.1	± 1.3	61.9
	Pinus cembroides	79.9	± 7.7	9.6
	J. pachyphloea	6.8	± 3.4	50.0
23	*P. edulis*	75.6	± 7.1	9.4
	J. pachyphloea	155.6	±11.6	7.5
	J. texensis	11.0	± 2.0	18.2
	Q. emoryi	20.2	± 9.6	47.5
24	*J. pachyphloea*	104.2	±10.9	10.5
	J. scopulorum	16.2	± 3.5	21.6
	P. cembroides	29.0	± 6.6	22.8
	Q. emoryi	13.3	± 6.3	47.4

for the two most important species of the type. For other plants also, Table II shows that those species providing an important proportion of the cover at a station had been adequately sampled there.

A similar table, not reproduced here, was based on numerical abundance of a species per line-strip. The per cent errors paralleled rather closely those based on cover. Again, small per cent errors cannot be attained for uncommon species with a reasonable number of sampling units.

The per cent ground cover furnished by each stratum was computed for each sampling station. The figures for the entire upper stratum, including tall shrubs as well as trees, range from 10.0 to 42.2 per cent. Markle (1952) indicates a combined cover of approximately 60 per cent for just *P. edulis* and *Juniperus* spp. at a station west of the divide near Grand Canyon, Arizona. The average of all stations studied in the present work is 23.3 per cent ground cover for the upper stratum and 18.8 per cent ground cover for the lower stratum. The sum of these figures is not an accurate estimate of total ground cover, since plants of the lower stratum occasionally occurred beneath the dominant trees.

The computed mean crown diameter of *P. edulis* from stations studied during the spring of 1953 is 9.0 ft. In comparison with the "over-mature" stand at Sta. 2 containing the largest *Pinus edulis* specimen in the world, the average stand elsewhere appears quite young. The figures are consistent among the stations, the mean crown diameter per station ranging only from 8.1 ft. to 10.4 ft. Within a given station, there is a peculiar uniformity in crown diameters, which appears to result from infrequent years of good ecesis and consequent scarcity of small trees, coupled with slow growth rate of the old individuals. Disturbances in the form of fire, grazing, disease and especially cutting have depleted the greater part of the association's largest trees.

Because of varying site conditions such as altitude, latitude, rainfall and soil conditions, it would be meaningless to attempt to average all the sampling stations to typify any one climatic subdivision. From field experiences and perusal of collected data, it is possible to choose a single station to represent its subdivision. Stations 6, 10, and 23 are considered typical of the northern, central and southern subdivisions respectively. Reference to these stations in Fig. 4 and Table I will clarify the following descriptions of the subdivisions.

Northern Subdivision

A typical pinyon-puniper stand in the northern subdivision contains in its upper stratum *P. edulis* in association with *J. scopulorum* and an admixture of one or two tall shrubs. Until its northern limit north of Fort Collins, Colorado, is reached, the pinyon component is usually of greater importance in the stand than any of its associates. North of Fort Collins, *J. scopulorum* becomes the dominant species with a few tall shrubs such as *Cercocarpus* spp., *Rhus trilobata,* and *Artemisia tridentata,* but without pinyon.

At sample station 6, pinyon and Rocky Mountain juniper occur in a ratio of approximately 7:1, but the former has more than 8 times the basal area. Sagebrush completes the upper stratum composition. Abundance figures give sagebrush, with nearly 20 per cent total abundance, a seemingly greater importance than *J. scopulorum* with only 10 per cent. However, when the cover figures are examined, the trees definitely show themselves to be dominant. Together the upper stratum furnishes 32.5 per cent ground cover or 14,161 square ft. per acre, 90 per cent of which is supplied by the two tree dominants.

An acre of ground in this stand carries about 150 trees with a total of 100 square ft. of basal area. The 135 pinyons per acre furnish about 90 square ft. of this amount with an average trunk diameter of 11 in.

Since this station was studied during the spring of 1953, before the herbaceous plants had fully developed, data were not accumulated for the lower stratum.

Other stations studied in the northern subdivision yielded similar results. In every instance except one, the pinyon component furnished several times the abundance and cover of the juniper component. At Sta. 7, *J. monosperma* is twice as abundant but about equal in cover quantities to pinyon.

Central Subdivision

The central portion of the range of pinyon-juniper east of the divide has by far the largest area of the three subdivisions. Because of the physiography of the region involved, great expanses of land suitable for this vegetation type are provided.

In general, the stands in this central subdivision contain *J. monosperma* in association with *P. edulis*. The former is usually the more abundant and in some cases is even found alone. Other species of trees enter the association as the altitude increases but this effect of altitude obscures the typical aspect. *Quercus emoryi* and *Q. undulata* are the principal oak associates; *Rhus trilobata* and *Cercocarpus* spp. sometimes contribute appreciable cover.

Sample station 10 exemplifies the attributes of the subdivision in general. Here *J. monosperma* is approximately twice as abundant as *P. edulis,* with respective per cent total abundance figures of 63.4 and 29.6. In association with these two dominants are found both *Q. emoryi* and *Q. undulata* which furnish a total abundance of 6.9 per cent.

The total abundance figure of the dominant tree species, pinyon and juniper, of 93 per cent compares closely with the 96.4 per cent total vegetation cover figure for the same species. The entire upper stratum covers 12.9 per cent of the ground or 5,384 square ft. per acre. Of this amount, 5,184 square ft. or 11.9 per cent is furnished by the dominants. Juniper provides twice the cover that pinyon does with approximately twice as many trees per acre (62.2:33.8).

The two dominants represent about 30 square ft. of basal area, measured at the 1 ft. level, per acre. This figure is composed of 21 square ft. of juniper and 9 square ft. of pinyon trunk area.

The balance of the central subdivision sample stations are similar in composition and cover. Stations 15, 16 and 17 do not correspond with typical stand figures since they were placed purposely at increasing altitudes to furnish data showing trends in composition with altitude. Sta. 8 shows an association composed of pinyon and juniper in a ratio of 3:1 but this is due to the effect of altitude at which the station was placed. This altitudinal effect upon composition is also reflected in the figures from Sta. 9 where the two components furnish approximately equal amount of both cover and abundance.

Southern Subdivision

The southern subdivision is very different in its composition from the other two subdivisions. Here occur *P. cembroides* and *J. texensis,* replacing *P. edulis* and *J. monosperma* typically found in stands farther north. The climate of the southern region differs significantly from that of the rest of the association range. Both the increased rainfall and the higher temperatures of spring begin one or two months earlier than in the central subdivision directly to the north. *J. pachyphloea* tends to dominate the association together with *P. cembroides, J. texensis* and *Quercus* spp.

The Davis Mountains in Texas are representative of this subdivision but areas near the northern climatic boundary grade into the type of association found more typically in the central subdivision.

Sta. 23 is representative of the type of stand encountered in this region. Here *J. pachyphloea* provides 61.2 and *P. cembroides* 28.1 per cent of the total abundance. Sta. 24 shows a similar disposition of dominants, but Sta. 22, with nearly 50 per cent of the total abundance furnished by *Q. greggii* and 16 per cent by *Q. emoryi* does not. All of the stations in this region carry considerable quantities of oak and in general bear out Weaver and Clements' (1938) designation of *"Quercus-Juniperus"* association.

At the typical station (23), the junipers and oaks furnish 71.0 per cent of the total vegetation cover. Of the 186.1 total trees per acre, junipers and oaks provide 135.7. This station has a greater per cent of the ground covered by the upper stratum (32.8) than the two other stations in the area (Sta. 22: 30.6, Sta. 24: 20.3).

P. cembroides is important although collectively the oaks and junipers outweigh it in abundance and cover values. It forms 29.0 per cent of the total vegetation cover and furnishes 4,138 of the total 14,287 square ft. of upper stratum cover per acre.

Sta. 20 and 21 are not typical of the southern subdivision. They represent the southernmost extension of the *Pinus-Juniperus* association typical of the central subdivision.

The phytographs (Fig. 4) reveal generally consistent differences in the phytosociological attributes of the stands among the three different subdivisions. The preeminent vegetational role of *Pinus edulis* in the northern subdivision, as contrasted with that of *Juniperus monosperma* in the central subdivision, is strikingly evident. The break in the size of the phytograph patterns between the northern and central subdivisions would have been much more abrupt had it not happened that Sta. 7 (northern) was located at the relatively low altitude of 6400 ft., while Sta. 8 and 9 (central) were established at much higher altitudes, 7100 and 7500 ft. This brought about an apparent reversal of the general trend.

Lower stratum

During the summer of 1952, only, was the lower stratum studied on a quantitative basis. Interceptions were recorded by species and these data later used in preparing a table of per cent ground cover, per cent vegetation cover and square ft. cover per acre, largely for 90 shrubby and herbaceous species (Woodin 1953). At no station did the total ground cover of the lower stratum exceed 28.9 per cent. At one station, the figure was as low as 4.1 but considering all the stations studied the average ground cover for the lower stratum is 18.8 per cent.

Of the total ground cover in the lower stratum, more than half is furnished by the grasses. The per cent of total ground cover of the lower stratum provided by various species of grasses varies

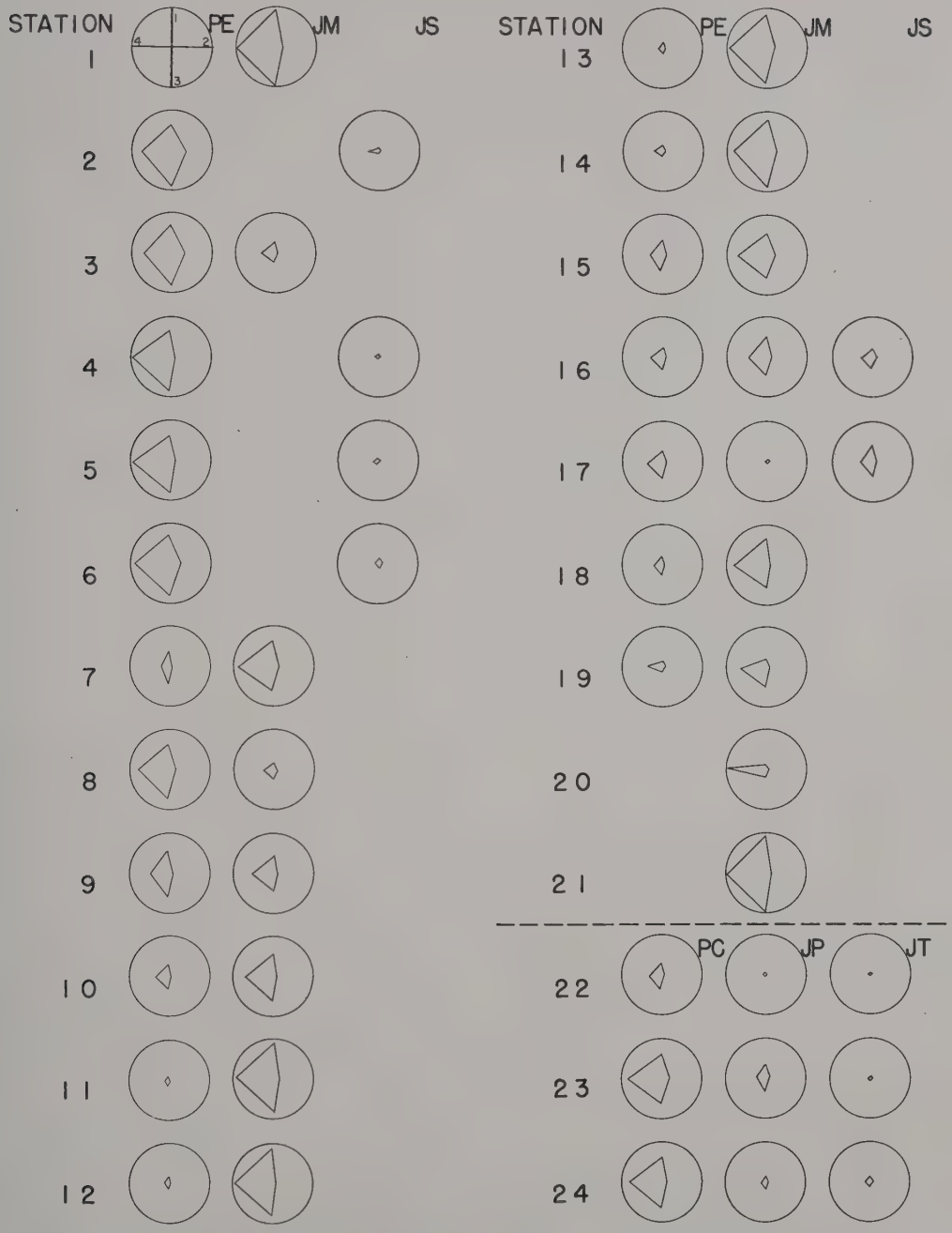

FIG. 4. Phytographs for the major tree species of the 24 sample stations. The various radii refer to: (1) % total abundance, (2) % ground cover (3) % vegetation cover, and (4) % of tree basal area of stems over 4 inches in diameter at 1 ft. above the ground. PE designates *Pinus edulis*, PC *Pinus cembroides*, JM *Juniperus monosperma*, JS *Juniperus scopulorum*, JP *Juniperus pachyphloea*, and JT *Juniperus texensis*. Stations 1-7 are in the northern subdivision, stations 8-19 are in the central, and 20-24 are in the southern subdivision.

from 24.6 to 89.0 per cent with an average of 59.1 per cent when all the stations are considered.

In general, the percentage of the ground covered by the lower stratum is less than that covered by the upper stratum. However at 4 stations the lower stratum provides more cover than does the upper.

Discussion and Conclusions

All conclusions in this paper are based upon cover values unless otherwise indicated.

Stratification

In the pinyon-juniper community there are three stata, two of which are recognized easily from a distance. The tree stratum includes the dominant individuals in the stand regardless of species. Between the trees, the intermediate or shrub story may be found. For purposes of cover classes this intermediate stratum was arbitrarily divided, in this study, at the 3 ft. level which, as would any height selected, sometimes included the same species in both upper and lower strata. The third and lowest stratum consists of grasses, forbs and rarely ferns and mosses. The two lower strata are seldom affected by shading from the dominant tree stratum but quite possibly their deep root systems are in competition for water with every neighboring vascular plant in the community.

Tree distribution and importance as related to climatic conditions

The climatic data from weather stations east of the continental divide have been separated into three groups. This division seems logical when the periods of precipitation are studied. The hythergraphs in Figure 2 show a definite variation as regards the first spring month to receive more than 1.5 in. of precipitation. This increase is not gradual; definite breaks appear between the data from stations in the three groups. This sharp increase in spring precipitation determines the period of vernal growth and flowering for many species.

Certain observations may be made concerning the climate of the region covered in the study:

1. From the hythergraphs (Fig. 2) it appears that differences in mean temperature during the growing season are unimportant in influencing the vegetation as compared with precipitation. The northern and central subdivisions have temperature means which are very similar for the same month from January through August, and practically identical from March through June. The average monthly precepitation, however, differs markedly. In the northern subdivision, although rainfall is well-spread through four months, its peak comes in April while low temperatures prevail. In the other two subdivisions, the peak of the rainy season comes late when the temperatures are high.

2. The initiation of the rainy period varies considerably with the three climatic subdivisions. In all three cases, only one month of the year shows at least 1 in. increase over the precipitation of the previous month. The northern subdivision has an increase of 1 in. during the month of April. A similar effect does not occur until July in the central subdivision and May in the southern.

3. Comparing amounts of rainfall from north to south, the spring period is progressively less moist, and the summer and fall more moist, southward.

4. The upper mean monthly temperature limit invariably occurs in July although in the southern subdivision June and August are almost equally warm. This value remains more or less constant at about 70° to 72° F. regardless of latitude.

5. The lower mean monthly temperature limit, while remaining the same for the central and northern subdivision is considerably warmer in the southern subdivision. This lower limit invariably occurs in the month of January.

6. There is a noticeable November dry period in every subdivision when compared with the precipitation during adjacent months and with the year as a whole.

The vegetation of the pinyon-juniper association tends to follow the climate of the three regional subdivisions used in this study. Quite naturally site conditions change with latitude and altitude but also exposure, relation to surrounding physiography and air current conditions have considerable effect upon distribution. The occurrence of a species outside the generally drawn limits given here does not necessarily reflect an oversight on the part of the authors, but rather an attempt to draw a line excluding unusually placed stands. Since the range of vegetational importance (Fig. 4) rather than the botanical distribution of the species is being considered, actual field observations provide the basis of the following conclusions.

P. edulis is found only in the central and northern subdivisions. Its place in the association is taken by *P. cembroides* farther south. The northernmost occurrence east of the divide is near Fort Collins, Colorado, which may be considered an unusual circumstance, Colorado Springs usually being given as the northern limit of this species.

J. monosperma is the foremost juniper component of the association in the central subdivision. It plays no significant vegetational role in either the northern or southern subdivisions except near their respective boundaries with the central sub-

division. Considering the stations in this study the only exception to this (Sta. 1) is found in the Big Horn Mountains on a level site, but this stand was surrounded by *J. scopulorum* on all sides. The vegetational range of *J. monosperma* can be said to be primarily in the central subdivision.

J. scopulorum occurs throughout the range of the association within the central and northern subdivisions. It tends to be found lower as the stations progress farther north while reflecting a moisture requirement higher than *J. monosperma* and even *P. edulis*.

P. cembroides is strictly limited to the southern one of the three subdivisions as defined in this paper. It is found only in limited quantities toward the northern limit of this subdivision.

J. texensis is also found only in the southern subdivision. Wherever *P. cembroides* was observed, *J. texensis* was in association with it. The southern subdivision is unique in that the first month with temperatures warm enough for the germination of tree seeds occurs one to two months earlier than in any other portion of the pinyon-juniper range east of the divide.

J. pachyphloea is found principally in the southern subdivision but is found at high altitudes in the central subdivision as well.

Differential moisture requirements

The paucity of tree species in pinyon-juniper, in comparison with other coniferous forest types, probably results from deficient moisture. The increasing moisture which accompanies increasing altitude is correlated also with an increase in the number of tree species. In the central subdivision, the *Juniperus monosperma* consociation occupies the lowest wooded sites. With increasing altitude, *Pinus edulis, J. scopulorum,* and *J. pachyphloea* successively attain importance. In the upper ecotone, all these species may occur, together with *Pinus ponderosa*.

Observations and community analyses indicate differing moisture requirements among the tree species. Usually it is not difficult to determine the relative moisture need in comparison with another species. The mesophily series in order of increasing water requirement is: *P. cembroides* and *J. texensis, J. monosperma, P. edulis,* and *J. scopulorum*.

The position of *J. pachyphloea* in the gradation has not been determined. It occurs in the southern subdivision with very warm climate species such as *P. cembroides* and yet is found as far north as the middle portion of the central subdivision actually associated with *P. ponderosa* in the upper ecotone. It would be expected to occur lower altitudinally as it occurred farther north but such is not the case. These facts agree with the observation of Lindsey (1951) that *J. pachyphloea* is influenced to a high degree by the substrate, as opposed to the climatic factor.

Altitudinal trends of component species

In order to demonstrate the altitudinal trends of the various components of the pinyon-juniper type, a graph of vegetation cover has been prepared for the trees (Fig. 5). In order to compare the stations which are located many miles apart latitudinally, a correction factor was used. Haviland (1926) states, "Generally speaking, the mean temperature falls 1° F. for each degree of latitude north (or south) of the equator; and the same for every three hundred feet of altitude." On this basis, since twenty miles of latitude are equal approximately to 100 ft. of altitude, the various stations were corrected to an "equivalent altitude" they theoretically might have if they were all located at the latitude (35°) of Albuquerque, New Mexico. All of the stations in the central subdivision have been considered, together with the station at Carlsbad, New Mexico, which, while actually in the southern subdivision, has the vegetational attributes of the central subdivision. Those stations located south of the 35° parallel were corrected by subtracting 100 ft. from their actual altitude and those north of it by adding 100 ft. for every twenty miles from the parallel.

Obviously this method does not take into consideration all factors which affect the altitudinal range of species. Nine of these stations are level (0-5 per cent slope) while the remaining four are on a moderate (15-30 per cent) slopes. In the case of the moderate slopes, the exposure is always toward the east. The use, in this connection, of stations representing two different slope classes might be criticized. However, Sta. 13 and Sta. 14, for example, which are immediately adjacent, have different slopes but quite similar vegetational attributes. At least in the central subdivision, 0-30 per cent differences in slope have little influence upon the composition of the stand if the sites are little different in altitude and close together.

Fig. 5 indicates that the genus *Juniperus* tends to decrease in its combined per cent vegetation cover while the commonest associate, *Pinus edulis,* tends to increase in value as the equivalent altitude increases. *Juniperus scopulorum* also increases in abundance with increase in altitude but does not enter the association until an altitude of about 6000 ft. or its equivalent latitudinally is reached. The increase in abundance of this species is very rapid with a small increase in altitude.

Often site factors influence the composition to

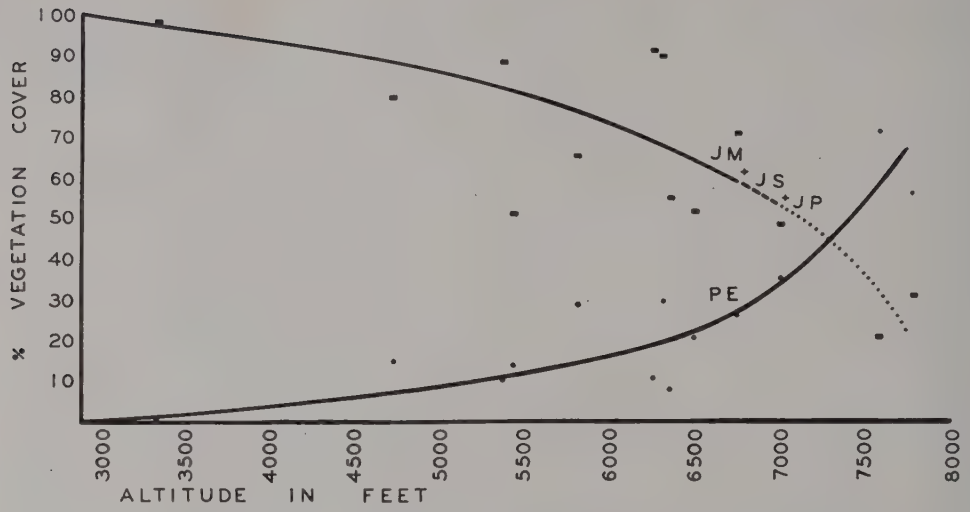

FIG. 5. Per cent vegetation cover of stations in the central subdivision plotted against the equivalent altitude each would assume at the latitude (35° N) of Albuquerque, New Mexico. The circular points represent the per cent vegetation cover furnished by *Pinus edulis*. The rectangular points represent that furnished by *Juniperus monosperma* (JM), *J. scopulorum* (JS), and *J. pachyphloea* (JP) on approximately the respective positions indicated by the solid, dashed, and dotted portions of the *Juniperus* curve. (See text for further explanation of equivalent altitude.)

such an extent that the various species components are found at altitudes differing widely from the normal. The graph brings out the noteworthy fact that not until 7200 ft. or its equivalent is reached do we find equal cover contributions by *Pinus* and *Juniperus*. Another graph using percentage abundance instead of cover showed the same thing. In general, then, there is more pinyon than juniper only in the upper 20 per cent of the altitudinal range of this type in the central subdivision. Up to approximately 5000 ft. the only dominant tree is juniper, constituting a consociation or consocies. At its upper limit, the type grades rather abruptly into the ponderosa pine type, with the lower edge of the ecotone at approximately 7500 ft. At this high altitude and above, in the ecotone between the woodland and the ponderosa pine, alligator juniper (*J. pachyphloea*) frequently occurs and indeed may enter the latter zone in considerable numbers.

Nomenclature

In the southern subdivision, which forms a part of the "*Quercus-Juniperus*" association of Weaver and Clements (1938), *J. pachyphloea* is more important than *P. cembroides*. The northern subdivision (Colorado east of the Divide) supports a *Pinus edulis-Juniperus scopulorum* community. Between these two lies the main body of the type in New Mexico, where *J. monosperma* is more important than *P. edulis* in the lower four-fifths of the altitudinal range. The predominant genus is customarily given first in type nomenclature.

Two woodland associations may be recognized for the eastern foothills of the Rockies from Texas to the southern boundary of Wyoming: (1) The *Quercus-Juniperus* association in West Texas and the extreme southern part of New Mexico. (2) The more northerly *Juniperus-Pinus* association in New Mexico and Colorado, which is subdivided into the *J. monosperma-P. edulis* faciation in New Mexico and the *P. edulis-J. scopulorum* faciation in Colorado. If a general term is required to cover the two associations in the area studied it should be "juniper-pinyon," since the one species of pinyon occurring in each association is less important there than a species of juniper. Probably the name of the entire woodland formation of the southwestern United States should be transposed to "*Juniperus-Pinus* Formation." Daubenmire (1943) used the category "juniper-piñon zone" for the woodland on both sides of the continental divide in the Rockies. From Woodbury's (1947) discussion of literature for Utah, it appears that *Juniperus* is the dominant genus in the woodland there. However, Billings (1951) points out that in the Great Basin of Nevada pinyon (*P. monophylla* T. and F.) is both more abundant and important than juniper.

Lower stratum

Throughout the range of the juniper-pinyon type, the lower stratum furnishes a rather small amount of cover. The spotty occurrence or com-

plete absence at stations of species to be expected there is largely brought about by overgrazing. The spread of exotic species into the range is facilitated where grazing is severe.

Overgrazing in arid lands promotes erosion also. On the average site studied, 81 per cent of the ground is not covered by the lower stratum; most of this is susceptible to erosion since it is not protected by any plant stratum.

Summary

Phytosociological studies of the juniper-pinyon vegetation type east of the continental divide were made on field trips during the summer of 1952 and spring of 1953. Twenty-four sampling stations within the type were used, from the Davis Mountains in Texas through the eastern foothills of the Rockies to the Big Horn Mountains in Wyoming. At each station, statistically reliable data were collected for cover and density expressions by the application of a newly devised sampling procedure called the "line-strip method."

Climatic data from records of Weather Bureau stations located within the juniper-pinyon type have been organized and summarized. On the basis of earliest significant spring rainfall, a breakdown of the range considered in this paper into at least three subdivisions is indicated. Vegetation data substantiates this breakdown which provides for:

1. A southern subdivision, including Texas and southeast New Mexico, which is entirely different in specific composition of the upper stratum from the remainder of the formation. Here occur *Juniperus pachyphloea, Pinus cembroides,* and *J. texensis,* the last two of which occur in no other portion of the range studied. Several oaks are also important.

2. A central subdivision which encompasses the State of New Mexico except the extreme southern part. This subdivision supports primarily *J. monosperma* and *P. edulis.*

3. A northern subdivision in Colorado in which *P. edulis* and *J. scopulorum* provide most of the upper stratum cover. This subdivision tends to intergrade somewhat in specific composition with the central subdivision.

The pinyon-juniper association at the latitude of Albuquerque, New Mexico (35° N. Lat.) reaches the point where pinyon and juniper furnish equal portions to the association at about 7200 ft. or its latitudinal equivalent. This association grades rapidly into the ponderosa pine zone at about 7500 ft. or its equivalent. Below 5000 ft. or its latitudinal equivalent, the vegetation of the type is a *J. monosperma* consociation. Because of the greater importance of the junipers when the three subdivisions are considered together, the type may be designated the juniper-pinyon or *Juniperus-Pinus* association in Colorado and New Mexico, and the *Quercus-Juniperus* association in western Texas.

References

Bauer, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology **24**: 45-60.

Beidleman, R. G. 1953. The island of pines. Living Wilderness **46**: 7-10.

Billings, W. D. 1951. Vegetational zonation in the Great Basin of western North America. p. 101-122 *in* C. R. du Colloque sur les bases écologiques de la régénération de la végétation des zones arides. U.I.S.B., Paris.

Buell, M. F., and J. E. Cantlon. 1950. A study of two communities of the New Jersey pine barrens and a comparison of methods. Ecology **31**: 567-586.

Canfield, R. H. 1941. Application of line interception method in sampling range vegetation. Jour. Forestry **39**: 388-394.

Daubenmire, R. F. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. **9**: 325-393.

Emerson, F. W. 1932. Tension zone between the grama grass and pinon-juniper associations in northeastern New Mexico. Ecology **13**: 347-358.

Haviland, M. D. 1926. Forest, steppe and tundra. Cambridge Univ. Press, London.

Lindsey, A. A. 1951. Vegetation and habitats in a southwestern volcanic area. Ecological Monog. **21**: 227-253.

Livingston, B. E., and F. Shreve. 1921. The distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Wash. Publ. **284**.

Merkle, J. 1952. An analysis of a pinyon-juniper community at Grand Canyon, Arizona. Ecology **33**: 375-384.

Pearson, G. A. 1920. Factors controlling the distribution of forest types. Parts I and II. Ecology **1**: 139-160, 289-311.

Penfound, W. T. 1945. A study of phytosociological relationships by means of aggregations of colored cards. Ecology **26**: 38-57.

Shantz, H. L., and R. Zon. 1924. Natural vegetation, map 1/8,000,000, *in* Atlas Amer. Agriculture, U. S. Dept. Agr., Washington, D. C.

Smith, A. D. 1940. A discussion of the application of a climatological diagram, the hythergraph, to the distribution of natural vegetation types. Ecology **21**: 184-191.

U. S. Forest Service. 1949. Areas characterized by major forest types in the United States (map, 1/5,000,000) U. S. Dept. Agr., Washington, D. C.

U. S. Dept. of Commerce. 1951. Climatological data, annual summary, New Mexico.

Weaver, J. E., and F. E. Clements. 1938. Plant ecology. 2nd ed. McGraw-Hill Book Co., New York.

Woodbury, A. M. 1947. Distribution of pigmy conifers in Utah and northeastern Arizona. Ecology **28**: 113-126.

Woodin, H. E. 1953. The pinyon-juniper association in the eastern foothills of the Rockies. Ph.D. thesis. Purdue University. (Listed in Dissertation Abstracts).

THE FOOD TURNOVER OF A BLUEGILL POPULATION[1]

SHELBY D. GERKING
Department of Zoology, Indiana University

INTRODUCTION

The growth rate of populations of aquatic organisms has become a dominating topic of limnological research, constituting the production problem. The trophic-level concept of Lindeman (1942) cut through the maze of data on aquatic food relations and pointed out the possibility that the quantitative aspect of production could be attacked by considering the energy content of the organisms and the energy flow from one trophic level to another. Lindeman's ideas have been justifiably criticized by Ivlev (1945), but, despite certain inadequacies, remain a significant contribution. The concept of production is still undergoing an evolution and is now in the process of refinement. Macfayden (1948) has traced the development of this concept and of closely associated ideas. Clarke (1946) considerably sharpened the working definitions of production rate, standing crop, and yield; as a result, terminology is becoming more stabilized.

The writer is particularly interested in fish production, feeling that investigation of this part of the aquatic ecosystem will contribute significantly to the general problem. The intrinsic biological interest of fishes and their considerable economic value are incentives to a more complete understanding of this part of the production process. Ricker (1946) accelerated the study of fish production by reviewing past achievements in this field and by pointing out areas for profitable research. The present work on the food turnover by a fish population was stimulated by Ricker's analysis of the subject.

The supply of food is one of the major, basic factors controlling the density and production of fishes. To understand more clearly the relationship between the fish population and its food supply, the efficiency of food conversion by sunfishes of various ages has been investigated in the laboratory. Experimental feeding of longear sunfish (*Lepomis megalotis*) and green sunfish (*Lepomis cyanellus*) was begun in 1950, and the results of these experiments have recently been published (Gerking 1952). The experiments have been continued, using the bluegill (*Lepomis macrochirus*) because it is widely distributed in the United States and because its population characteristics are more completely known than are those of other species in our region.

For our purposes, growth is defined as the synthesis of new protoplasm. Since the synthesis of protein is the most characteristic feature of growth, protein accumulation is used as the index of the efficiency of the growth process. There are objections against using other possible indices, such as wet weight, dry weight, weight of organic matter, fat, and carbohydrate. Wet weight has the obvious disadvantage that water content varies considerably under different conditions of nutrition. Dry weight and weight of organic matter (dry weight minus ash weight) are not true reflections of growth because the quantity of fat varies tremendously. Under experimental conditions fat has been found to vary between 3 and 33 per cent of the dry weight. The variability is almost as great under natural conditions. Bluegills from a northern Indiana lake have been sampled at all seasons for two years and the fat content has varied from 8 to 33 per cent of the dry weight. Neither is true growth reflected by the caloric content of the body as measured by a bomb calorimeter. The variability in the quantity of fat is again the complicating factor, especially since fat has the greatest caloric value of the three principal organic materials. Other aquatic organisms may or may not be as variable as fish in this respect, but the difficulty should be appreciated when estimating "energy flow" through a food chain. The accumulation of fat by fish is no indication of the actual amount of material being synthesized in the growth process. Fat is generally deposited in practically the same molecular arrangement as it occurs in the food (Lovern 1951). Carbohydrate is not stored in the animal body to any appreciable extent and cannot be used to indicate growth.

Protein turnover will be defined as the amount of protein that is required by a population for growth, for the metabolic expenditure of energy, and for the replacement of proteins broken down during the normal course of living. Protein turnover is thus synonymous with the amount which is absorbed by the intestinal tract except that it describes the various uses which are made of the protein within the body. To illustrate the

[1] Contribution No. 532 from the Department of Zoology, Indiana University.

computation of protein turnover, the vital statistics of the bluegill population of Gordy Lake, Indiana, will be used. Estimates of the abundance and mortality rates of this population have been completed (Gerking 1953), and its growth rate has been investigated more thoroughly since that time. The variables of abundance, growth, mortality and efficiency of protein utilization for growth will be combined to procure an estimate of protein turnover by the population.

Population Estimates

The bluegill population of Gordy Lake was estimated by Petersen and by Schnabel methods, using the fishermen's catch to determine the ratio of marked to unmarked fish in the lake. The population estimates presented here are based on the same data as in the previous study, but they have been reassembled. A rigorous examination of the estimates was made in the earlier paper and will not be repeated here. All estimates apply to the month of June.

A fair number of age II fish were caught in cylindrical wire traps, and it was possible to estimate their abundance by the Schnabel method, using only trap-caught fish. The traps sampled age II bluegills ranging in size from 90 to 115 mm. There is no information about a group of age II fish smaller than 90 mm. An estimate of 5300 will be referred to as "age II," although it represents only a part of that age-group.

Age III and age IV numbered about 8850. A considerable size overlap between the age-groups prevented separate estimates of abundance. The total number was apportioned between the two ages by using the relative frequency of each age in a large sample of the fishermen's catch. Of 798 fish assigned to the two ages by scale reading, 446 were age III and 352 were age IV. The population assigned to age III thus becomes 4950, and that of age IV is 3900. Not quite all of the age III fish were vulnerable to capture at the time sampling began. The sample is slightly biased in favor of the age IV fish, but this method of apportioning the population estimate seems to be as accurate as possible under the circumstances.

There was an estimated 1315 fish of ages V to VIII. The catch sample included 58 age V, 16 age VI, 4 age VII, and 1 age VIII. The population of this group was distributed according to the proportion of each age in the catch as follows: 965 age V, 266 age VI, 67 age VII and 16 age VIII.

Mortality Rates

The total annual mortality rate was estimated to be 72.5 per cent by comparing the number of individuals of successive ages in the catch (Fig. 1). This is somewhat lower than the annual mortality rate estimated in the earlier paper, and it is apparently a more accurate interpretation of the data. Age III fish were almost completely vulnerable to fishing when the samples were taken, and they have been included in the computation.

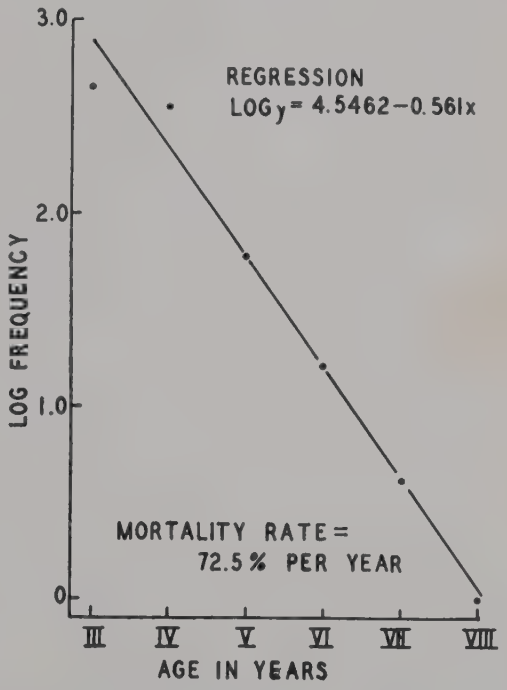

Fig. 1. Total annual mortality rate of the bluegill population of Gordy Lake, Indiana, calculated from the relative frequency of each age in the catch.

Age IV was a strong year-class in the population in 1950. These factors influence the estimation of mortality rate, but the regression agrees with the constant mortality rate affecting ages V to VIII.

The rate of exploitation, *i.e.* the annual expectation of death from fishing, was determined by recaptures from a known number of marked fish in the lake. The vulnerable population was removed at a rate of 32.2 per cent from June 2 to September 4. The winter and late fall fishing, although not observed, was known to be small. The yearly rate of exploitation was estimated to be only slightly above the summer rate, or about 35 per cent. The annual expectation of natural death is $72.5 - 35.0 = 37.5$ per cent.

In calculations which follow it is desirable to express these mortality rates as instantaneous rates, following the methods developed by Ricker (1944). Conversion to instantaneous rates is the

only practical method so far devised to combine growth and mortality rates. The definitions of certain symbols are repeated here.

a = total annual mortality rate
i = total instantaneous mortality rate
μ = rate of exploitation (annual expectation of death from fishing)
υ = annual expectation of natural death
p = instantaneous mortality rate from fishing
q = instantaneous mortality rate from natural causes

The determination of instantaneous rates from the empirical data becomes:

(1) where $a = 0.725$, $i = 1.29$

(2) since $\frac{i}{a} = \frac{p}{\mu}$, then $p = \frac{1.29 \times 0.350}{0.725} = 0.623$

(3) since $\frac{i}{a} = \frac{q}{\upsilon}$, then $q = \frac{1.29 \times 0.375}{0.725} = 0.667$

By definition, $a = \mu + \upsilon$, and $i = p + q$. The instantaneous total mortality rate was taken from Ricker's (1948) tables.

Age and Growth

Age and growth of the Gordy Lake bluegills have been analyzed by standard methods, employing scale reading for age determinations. The scales were unusually well marked, and the age assessment was relatively simple. The radius of the anterior field of the scale and the distance from the focus to each annulus were measured. The fork length of the fish at the time of capture is essentially proportional to the anterior radius of the scale, with the intercept of the x and y axes at 20 mm. (Ricker 1942). The length of individual fish at each annulus was calculated as follows:

$$\text{Fork length of fish at time of annulus formation} = 20 + \frac{(\text{scale radius at year x})\ (\text{fork length} - 20)}{\text{total scale radius}}$$

The fork lengths were converted to weights from a length-weight graph, and the average weight of the fish at each age was computed. The maximum age in our sample was age VIII. The weight at age IX was extrapolated in order to estimate the growth of the fish during the last year of life.

The instantaneous rate of growth in terms of weight, k, is a useful statistic for relating growth and mortality. The k values were found by plotting age and the logarithms (base 10) of the weight at each age (Fig. 2). Free-hand tangents to the resulting curve were drawn midway between successive ages. The slope of each tangent was converted to natural logarithms by multiplying by 2.30. This method is the same as that employed by Ricker (1945) for a somewhat different purpose.

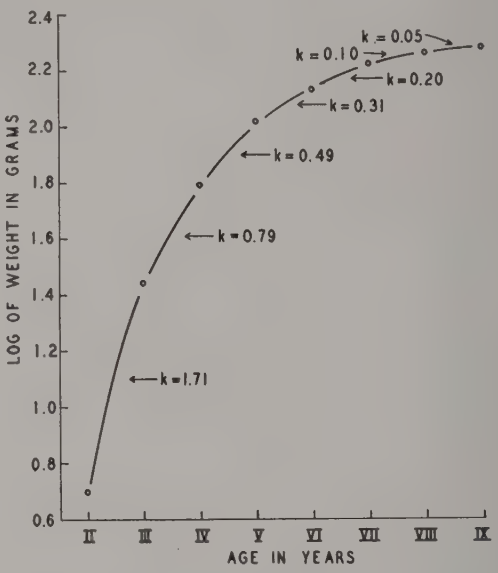

Fig. 2. Method of computing instantaneous rate of growth, k, for the bluegill population of Gordy Lake, Indiana. See text for further explanation.

Protein Utilization

The efficiency of protein utilization for growth by bluegills of various ages was determined by feeding the fish a weighed amount of meal worms (*Tenebrio mollitor* larvae) each day for 50 days. Meal worms were selected as food because they simulate the insect larvae which compose a large share of the bluegill diet in nature. Protein nitrogen was estimated in the food and feces by the Kjeldahl method. The amount of protein retained during feeding was found by measuring the dry weight and nitrogen content of fish at the beginning and end of the experiment. A group of sample fish represented the experimental group at the start of feeding. The efficiency of protein utilization for growth was calculated by relating the amount of protein nitrogen retained to the amount of protein nitrogen absorbed. The efficiency of protein utilization decreases as the fish increase in size (Fig. 3). A semi-logarithmic transformation of the data seems most appropriate, and the regression has been calculated in this way.

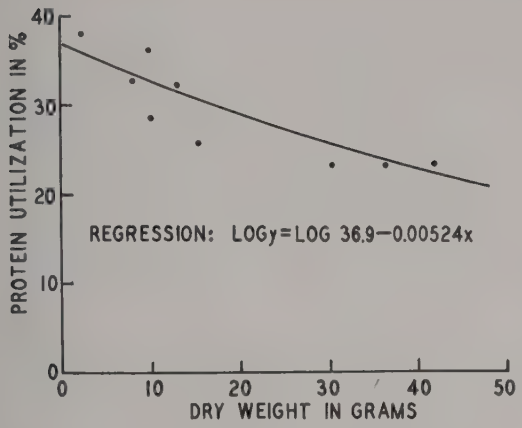

FIG. 3. The relationship between the dry weight of bluegills and the utilization of protein for growth. The fish were fed meal worms in 50-day aquarium experiments.

The amount of protein required for growth by individual fish having the characteristics of Gordy Lake bluegills can be estimated (Table I) by utilizing the age-growth data and the efficiencies of protein utilization as related to the size of the fish. The wet weight of the fish at each age was converted to dry weight by assuming that the dry substance makes up 27.8 per cent of the wet weight. This percentage was derived by averaging many dry weight measurements of bluegills taken from several sources during the past three years. The protein content, 61.25 per cent of the dry weight, is based on the same observations. The efficiency of protein utilization was calculated for each age from the regression equation of Figure 3. For example, the average dry weight of age II fish in their third year of life is about 3.6 g. (0.278 × average weight of age II fish from Figure 2, 13.0 g.). The efficiency of protein utilization is calculated as follows:

$$\log y = \log 36.9 - 0.00524 \times 3.6 = 1.5484,$$
$$y = 35.4 \text{ per cent}$$

Variability is associated with each column of the table, and estimates of reasonable accuracy have been chosen.

TABLE I. *Estimate of the protein turnover by individual fish of the Gordy Lake bluegill population. Weight at each age was calculated from age-growth determinations.*

Age	Weight	Dry weight*	Protein**	Protein gain	Efficiency of protein utilization	Amount of protein required for growth
	g.	g.	g.	g.	%	g.
II....	5	1.4	0.86			
				3.92	35	11.21
III....	28	7.8	4.78			
				5.76	32	18.03
IV....	62	17.2	10.54			
				7.35	28	26.24
V....	105	29.2	17.89			
				5.26	25	21.04
VI....	136	37.8	23.15			
				5.45	22	24.80
VII....	168	46.7	28.60			
				2.58	21	12.28
VIII....	183	50.9	31.18			
				1.53	20	7.65
IX....	192	53.4	32.71			

*Dry weight assumed to be 27.8 per cent of wet weight.
**Protein assumed to be 61.25 per cent of dry weight.

Variability is associated with each column of the table, and estimates of reasonable accuracy have been chosen.

The data can also be construed as representing the amount of protein turnover by an individual fish from age II to age IX, or 121.25 g. Estimates made for fish of age 0 and age I increase this amount by 2.5 g. A total of 123.8 g. of protein would, therefore, be required to produce a fish containing 32.7 g. of protein, an average efficiency of 26 per cent. This average efficiency is an overestimate because the amount of "replacement protein" has not been included in the computations. The determination of replacement protein requires separate laboratory analysis which has yet to be done.

Replacement protein may be a significant quantity. It is required at all times, and it probably varies with temperature. Growth does not occur in the winter among bluegills, although they feed in cold weather (Moffett and Hunt 1945). The protein consumed during the winter would be used only for energy expenditure and replacement.

No correction for unabsorbed protein has been made. In our experiments only 2 per cent of the protein nitrogen fed to the fish was found in the feces and a part of this can undoubtedly be accounted for by the "metabolic nitrogen," *i.e.* nitrogen derived from digestive juices and epithelial cells abraded from the alimentary canal. For practical purposes, the protein consumed by the fish is equivalent to that absorbed.

FOOD TURNOVER BY THE POPULATION

The four estimates of growth, mortality, abundance and protein utilization can now be combined to provide a measure of the protein turnover by the population (Table II). It will be convenient to obtain a value for the average population during the summer, and Ricker (1944, 1945) has provided the mathematical treatment necessary for this computation. The following relationships are of primary interest:

(4) $k - i = g$, where g is the net instantaneous rate of increase in weight of an age-group.

(5) $e^g - 1$ = the fractional net increase in weight of an age-group.

(6) $\frac{e^g - 1}{g} \times$ initial weight of an age group = the average weight of an increasing age-group.

The weight of the population at the beginning of the summer is found by multiplying the abundance of each age-group by the average weight of the individuals of that group as determined from the age-growth data. The average number in each age-group during the summer is estimated by dividing its average weight by the mean weight of the individuals of that group. The mean weight of the individuals in each age-group was read from Figure 2 at a point mid-way between successive ages. The protein turnover by a single individual in each age-group (Table I) is multiplied by its average population to provide an estimate of the protein turnover for that age-group. The total protein turnover for the whole population during its season of growth is found by summing the protein required by all age-groups.

One of the notable features of the Gordy Lake population is that none of the age-groups from III to VIII shows a net increase under the observed conditions of growth and total mortality. Growth is not adequate to compensate for the rate of mortality. On the other hand, growth exceeds mortality among age II fish, primarily because less than half of them became vulnerable to fishing. The instantaneous rate of total mortality of age II fish, 0.54, was based on the rate of exploitation of these fish (4.5 per cent) and the rate of natural mortality corresponding to older fish.

Our method of calculation shows that 156.8 kg. of protein are required by the population during the summer growth period. The source of this protein is, of course, the various organisms which comprise the food of the bluegill, and it is worthwhile to attempt to estimate the total weight of organisms which this amount of protein represents. For this purpose, the excellent data of Geng (1925) are available. He analyzed various aquatic organisms for water, protein, chitin, fat, carbohydrate, and ash. The average protein content of 24 different organisms listed by Geng was 9.59 per cent of the live weight. (Geng's tabulation of "raw protein" rather than "true protein" has been used because the data are more extensive, and the small difference between the two is unimportant in the estimations which are made.) The approximate weight of organisms consumed by the population is $\frac{1}{0.0959} \times 156.8 = 1635.0$ kg. (3597 pounds). The area of Gordy Lake is 11.5 hectares, and on a relative basis the bluegill population consumed some 142 kilograms of organisms per hectare (126 pounds per acre).

Catch and Natural Mortality

The rate of exploitation and expectation of natural death are known for the Gordy Lake population and the estimates of deaths from these sources will be presented since they offer partial confirmation of the previous computation. The estimated catch can be secured by multiplying the average weight of each age-group by the instantaneous mortality rate from fishing (p), which applies to the appropriate age-group, and summing the entries (Table III). A total of 233.2 kg. (513.0 lbs.) make up the catch as estimated

Table II. *Estimate of the protein turnover by the Gordy Lake bluegill population in 1950.*

Age	k	i	g	$e^g - 1$	Beginning of summer			$\frac{g-1}{g}$	Average during summer			Protein turnover by each individual *g.*	Protein turnover by population *kg.*
					Population	Individual weight *g.*	Population weight *kg.*		Population weight *kg.*	Individual weight *g.*	Population		
II	....	....	.....	.....	5300	5	26.5						
	1.71	0.54	+1.17	+2.232	....	..	....	1.899	50.3	14	3590	11.21	40.2
III	....	....	.....	.....	4950	28	138.6						
	0.77	1.29	−0.52	−0.406	....	..	....	0.781	108.2	42	2580	18.03	46.5
IV	....	....	.....	.....	3900	62	241.8						
	0.49	1.29	−0.80	−0.551	....	..	....	0.689	166.6	80	2080	26.24	54.6
V	....	....	.....	.....	965	105	101.3						
	0.31	1.29	−0.98	−0.625	....	..	....	0.638	64.6	120	538	21.04	11.3
VI	....	....	.....	.....	266	136	36.2						
	0.20	1.29	−1.09	−0.664	....	..	....	0.609	22.0	153	144	24.80	3.6
VII	....	....	.....	.....	67	168	11.3						
	0.10	1.29	−1.19	−0.696	....	..	....	0.585	6.6	176	38	12.28	0.5
VIII	....	....	.....	.....	16	183	2.9						
	0.05	1.29	−1.24	−0.711	....	..	....	0.575	1.7	188	9	7.65	0.1
IX	....	....	.....	.....	....	192							
					15,464	....	558.6	....	420.0	....	8979	....	156.8

by this method. The actual catch was 267.7 kilograms (589.6 pounds) of bluegills, based on an intensive creel census. Our estimate is 12.9 per cent lower than the observed amount. On a relative basis the estimated catch was 20.2 kilograms per hectare (18.0 pounds per acre) and the actual total was 23.2 kilograms per hectare (20.7 pounds per acre), a difference of 3.0 kg. per hectare.

TABLE III. *Estimation of the total catch and the weight of fish which died from natural causes in the Gordy Lake bluegill population.*

Age	Average Population Weight *kg.*	Instantaneous rate of fishing mortality *p*	Catch Weight *kg.*	Instantaneous rate of natural mortality *q*	Died from Natural Causes *kg.*
II	50.3	.058	2.9	.481	24.2
III	108.2	.623	67.4	.667	72.2
IV	166.6	.623	103.8	.667	111.1
V	64.6	.623	40.2	.667	43.1
VI	22.0	.623	13.7	.667	14.7
VII	6.6	.623	4.1	.667	4.4
VIII	1.7	.623	1.1	.667	1.1
IX					
Total.	....	....	233.2	....	270.8

Since there is no method of checking the food turnover by the population, such good agreement in a part of the over-all computation is gratifying. The discrepancy between the estimated catch and actual catch may be accounted for by the fact that average weights for individual age-groups were back-calculated to the time of annulus formation in May, while the population estimates were made in June. The growth which occurred during this month has not been considered, and the average population weight should be somewhat higher than is shown in Tables II and III. This error could be corrected by further refinement, but it would be of doubtful significance in this case.

The weight of fish which died from natural causes can be computed similarly to that just described, by substituting q, the instantaneous rate of mortality from natural causes, for p. The fish which died in the lake during 1950 were 270.8 kg. or 595.8 pounds.

Appraisal of Possible Sources of Error

Sampling errors. All the basic data used in the calculations of population size, growth, and mortality are subject to sampling error (Ricker 1948; Hile 1941). Apparently these errors have been kept at a minium in the present estimates, but they should not be overlooked.

Timing of growth and mortality. It has been assumed that growth and mortality coincide in time. This assumption needs to be examined critically because it has an important bearing on the dynamics of fish populations. Methods are available for treating population data when the timing of growth and mortality is established.

Application of laboratory data to the field situation. The application of the laboratory experiments on protein utilization to the natural situation deserves to be examined carefully. Obviously, the measurements of growth efficiency can be made with more precision in the laboratory than in the field. The laboratory methods used are common in agricultural nutrition work (Maynard 1951), although they have never before been applied to fishes. The technical difficulties of working with an aquatic animal have been largely overcome but certain refinements are still to be desired.

The genetic influence on the growth efficiency of fishes has not been appraised critically. Different races of fish may respond differently to the same food, since there are indications that the utilization of protein for growth is genetically variable. Recently, Prather (1951) accomplished an improvement in the efficiency of food conversion in the largemouth bass, *Micropterus salmoides,* by selective breeding. In trout culture it is common practice to select fast-growing races for hatchery breeding, and the growth of domestic animals has been greatly improved by selective breeding programs. In our experiments the bluegills used in the laboratory were from Yellowwood Lake, near Bloomington, Indiana—not from Gordy Lake. A genetic difference between these races in the ability to utilize protein for growth would alter the estimate of the food turnover.

The laboratory experiments were performed in summer at room temperature (average = 25.9° C.) which is higher than lake temperatures generally encountered at the same time of year. Food intake is affected by temperature (Markus 1932), but the effect of temperature upon the *rate* at which food is utilized for growth remains a most important subject for future investigation. By analogy, the efficiency of protein utilization is not expected to vary much with temperature on the basis of Terroine and Wurmser's (1922) work on *Aspergillus niger*. They observed that the coefficient of utilization of glucose $\left(\frac{\text{weight increase of mycelium}}{\text{glucose consumed}}\right)$

was the same over a temperature range of 22-38° C.

As far as the food is concerned, meal worms probably resemble the natural food of the bluegill as well as can be done in the laboratory. Live food is likely to contain sufficient vitamins and other growth factors, although aquatic organisms may be better or worse than meal worms in this respect.

High rates of feeding were employed in the laboratory. The experimental fish were fed at the rate of approximately 3 per cent of their body weight per day. This is very close to the maximum food intake under the conditions of our experiments. The amount of protein used for growth depends in part upon the intake of protein above the amount needed for energy requirements. The efficiencies reported here, based on near-maximum food consumption, therefore represent nearly maximum efficiencies. Whether bluegills in nature eat such large quantities of food is not known, but some indirect evidence indicates that they do. A comparison of the linear growth increments of the laboratory bluegills and those from Gordy Lake (Fig. 4) shows that both groups were growing at about the same rate. Consequently, the rate of food consumption must have been approximately the same in the two groups.

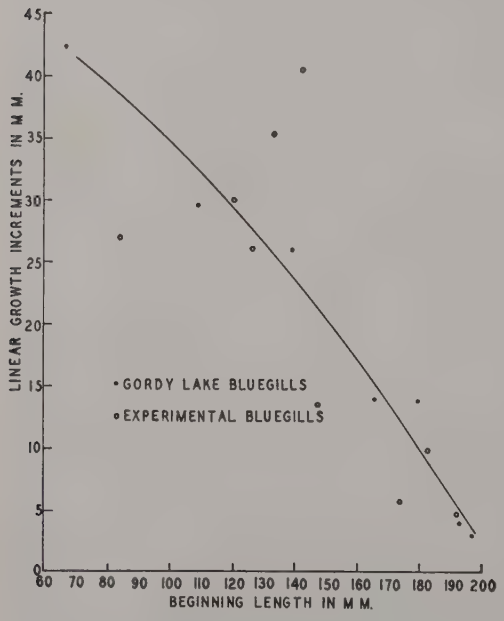

FIG. 4. The relation between linear growth increment and the size of fish at the beginning of a growth period. Data for Gordy Lake bluegills were taken directly from age-growth analyses, and the freehand regression is based on this information. The growing season lasts about 150 days in nature. Growth increments of fish in 50-day feeding experiments have been multiplied by 3 to approximate the total growth which might have been achieved in a natural growing season.

DISCUSSION

The selection of food by the bluegill has received considerable attention. Ball (1948) demonstrated that insects are the most important food organisms found in the diet and that the aquatic forms are derived almost entirely from the littoral zone. About 50 per cent of the diet was composed of plants, zooplankton and terrestrial insects. Parks' (1949) analysis of the bluegill diet showed that 24 per cent of the food included the latter food items. Vascular aquatic plants were found to be an important constituent of the diet in both studies, and Ball showed that plant consumption varied inversely with the amount of invertebrates in the lake. McCormick (1940) also presented evidence that bluegills eat considerable quantities of higher aquatic plants (49 per cent), and other studies have confirmed this fact still further. Plants are not consumed incidentally in the process of capturing animal food. Ball wrote, "In the great majority of cases when the stomach contained *Najas,* there was no other food present, and the individual leaves were nearly of the same length, as if they had been cropped off intentionally. . . ." It remains to be learned whether aquatic plants contribute significantly to the protein requirement of the bluegill. About 2-20 per cent of the food comes from terrestrial sources.

Regardless of its source, about 157 kilograms of protein which were consumed by the bluegills must have originated in the lake or entered from the outside. This represents the turnover of protein by the population, not the total available supply. The total protein turnover by the bluegill population can be partitioned as follows (Table IV): 47.9 kilograms were used for growth and about 108.9 kilograms were used to contribute to the metabolic expenditure of energy. Replacement protein has not been included for reasons mentioned above. The nitrogenous excretory products resulting from protein catabolism are soluble in water and become available for use by other organisms in the aquatic nitrogen balance. These products are for the most part simple molecules (Smith 1929) and can be utilized quickly. Our own analyses have shown that ammonia makes up about 60 per cent of the total nitrogen excreted by bluegills.

The protein incorporated into the bodies of the bluegills themselves can also be partitioned.

TABLE IV. *Partition of protein and protein nitrogen consumed by the bluegills of Gordy Lake, Indiana, into various segments of the aquatic nitrogen cycle. Values apply to the bluegill population from age II to age VIII.*

Item	Partition	Protein		Protein nitrogen*	
		kg.	lbs.	*kg.*	lbs.
1	Consumed	156.8	345.0	24.3	53.5
2	Used for growth	47.9	105.4	7.4	16.3
3	Used for metabolism	108.9	239.6	16.8	37.0
4	In fish which died from natural causes	46.0	101.2	7.2	15.8
5	In catch	39.6	87.8	6.3	13.4
6	In average standing crop	71.4	157.1	11.2	24.6

Explanation of above items:

1. From Table II.
2. Summation of items in column 5, Table I, times average population of each age-group, Table II.
3. Item 1 minus item 2.
4. From Table III, converted to protein by multiplying by 17 per cent.
5. Same as preceding statement.
6. From Table II, converted to protein as above.

*Protein × 0.16=protein nitrogen.

Angling removed 39.6 kilograms which represents a permanent loss to the lake. The 46.0 kilograms of protein in the fish which died from natural causes can be utilized directly by scavengers, and the products of bacterial decomposition can be used by other organisms. A small quantity of this protein may be removed from the lake by predators such as fish-eating birds and mammals.

From this point of view, our information contributes to the quantitative relationships in the nitrogen balance of the aquatic environment. Exploitation by man plus a small unknown amount removed by birds, etc. represents the only significant loss of nitrogen from the biomass. Bluegills were by far the dominant species in the Gordy Lake catch and the protein nitrogen loss from this source was only 6.3 kilograms or 0.55 kilograms per hectare. Rain, run off, inorganic wind-blown material, and leaf-fall could probably replace this loss. It has been gradually realized from other studies that nitrogen is not the limiting factor in aquatic productivity, and these data are in keeping with that opinion.

Recruitment has not been taken into consideration in the computation. The young fish, which were not sampled, are growing rapidly and adding to the total protein of the population. The potential recruitment required to maintain the average standing crop is indicated by the partition of Table IV. Natural deaths accounted for 46.0 kg. of protein and 39.6 kg. were removed by fishing, a total of 85.6 kg. At the same time, 47.9 kg. of protein were added to the population in growth. The net decrease in the population is therefore $85.6 - 47.9 = 37.7$ kg. of protein, which is about one-half the average standing crop (71.4 kg.). In order to maintain the standing crop, 33.7 kg. of protein must be added to the population by growth, principally by the younger age-groups.

The objective of quantitative studies of the food chain is to establish some measure of the "ecotrophic coefficient" (Ivlev 1945), which is defined as the fraction of the production of a food organism which is actually consumed. Ivlev stressed the importance of individual species of food organisms. Our calculation of the food turnover has not been so specific, but it is a step toward the accomplishment of the same general purpose. The efficiency of productivity will be more completely understood when the relationship between the food turnover and the total food supply is known.

SUMMARY

The food turnover of the bluegill (*Lepomis macrochirus*) population of Gordy Lake, Indiana was estimated by emphasizing the role of protein in the nutrition of fishes. Protein turnover is defined as the amount of protein that is required by a population for growth, for the metabolic expenditure of energy, and for the replacement of proteins broken down during the normal course of living. The efficiency of protein utilization for growth was determined by experiments on bluegills in the laboratory. Field studies provided information about the vital statistics of the Gordy Lake population. The protein turnover was computed by combining measurements of protein utilization, growth, mortality and the population of bluegills in the lake.

It was estimated that about 156.8 kg. of protein were consumed by the bluegill population in 1950. About 47.9 kg. of protein were added to the population in growth, and the remainder (108.9 kg.) was used for the metabolic expenditure of energy. No estimate of replacement protein could be made. The total amount of food organisms which was represented by the protein turnover was computed from an average percentage of protein in the living weight of various aquatic animals (9.59 per cent). On this basis the total amount of food organisms consumed by the bluegill population was 1635.0 kg. or 142 kg. per hectare (126 pounds per acre).

A contribution to the aquatic nitrogen cycle was made by partitioning the protein in the average standing crop of bluegills into various segments. Natural deaths accounted for 46.0 kg. of protein, and 39.6 kg. were removed from the lake by fishing. Since 47.9 kg. of protein were added to the population by growth, the net decrease in

population protein was $(46.0 + 39.6) - 47.9 = 37.7$ kg. of protein. Recruitment must make up for this net decrease in order to maintain the average standing crop of 71.4 kg. of protein. Under the observed conditions of mortality and growth, recruitment must replace about one-half the average standing crop per year.

References

Ball, Robert C. 1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. Mich. St. Coll., Ag. Exp. Sta., Tech. Bull. No. 206: 2-59.

Clarke, George L. 1946. Dynamics of production in a marine area. Ecol. Monogr., **16**: 321-335.

Geng, Hugo. 1925. Der Futterwert der natürlichen Fischnahrung. Zeit. für Fischerei, **23**: 137-165.

Gerking, Shelby D. 1952. The protein metabolism of sunfishes of different ages. Physiol. Zool., **25**: 358-372.

———. 1953. Vital statistics of the fish population of Gordy Lake, Indiana. Trans. Am. Fish. Soc., **82**: 48-67.

Hile, Ralph. 1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Trans. Wis. Acad. Sci., Arts and Letters, **33**: 189-337.

Ivlev, V. S. 1945. The biological productivity of waters. (Translation by W. E. Ricker.) Adv. Mod. Biol., **19**: 98-120.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, **23**: 399-418.

Lovern, J. A. 1951. The chemistry and metabolism of fats in fish. *In:* Biochemical Society Symposia No. 6, Cambridge University Press, pp. 49-62.

McCormick, Elizabeth M. 1940. A study of the food of some Reelfoot Lake fishes. Jour. Tenn. Acad. Sci., **15**: 64-75.

Macfadyen, A. 1948. The meaning of productivity in biological systems. J. Anim. Ecol., **17**: 75-80.

Markus, Henry. 1932. The extent to which temperature changes influence food consumption in largemouth bass (*Huro floridanus*). Trans. Am. Fish. Soc., **62**: 202-210.

Maynard, Leonard A. 1951. Animal Nutrition. New York: McGraw-Hill, ix. + 474 pp.

Moffett, J. W. and Burton P. Hunt. 1945. Winter feeding habits of bluegills. *Lepomis macrochirus* Rafinesque and yellow perch, *Perca flavescens* (Mitchill), in Clear Lake, Washtenaw County, Michigan. Trans. Am. Fish. Soc., **73**: 231-242.

Parks, C. E. 1949. The summer food of some game fishes of Winona Lake. Investigations of Indiana Lakes and Streams, **3**: 235-245.

Prather, E. E. 1951. Efficiency of food conversion by young largemouth bass, *Micropterus salmoides* Lacépède). Trans. Am. Fish. Soc., **80**: 154-157.

Ricker, W. E. 1942. The rate of growth of bluegill sunfish in lakes of northern Indiana. Investigation of Indiana Lakes and Streams, **2**: 161-214.

———. 1944. Further notes on fishing mortality and effort. Copeia, **1944**: 23-44.

———. 1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia, **1945**: 84-94.

———. 1946. Production and utilization of fish populations. Ecol. Monogr., **16**: 373-391.

———. 1948. Methods of estimating vital statistics of fish populations. Ind. Univ. Publ., Sci. Ser. No. 15. 1-101 pp.

Smith, Homer. 1929. The excretion of ammonia and urea by the gills of fish. Jour. Biol. Chem., **81**: 727-742.

Terroine, Emil F. and René Wurmser. 1922. L'énèrgie de croissance I. le developpement de *l'Aspergillus niger*. Bull. de la Société de Chimie Biologique, **4**: 519-567.

A STUDY OF SOME OF THE FACTORS AFFECTING THE NATURAL REGENERATION OF TAMARACK (*LARIX LARICINA*) IN MINNESOTA[1]

DONALD P. DUNCAN[2]

School of Forestry, University of Minnesota, St. Paul 1, Minnesota

Introduction

Sound management of any renewable natural resource upon which man is dependent for his well-being involves sustained yield. Land economically suited to the production of some particular commodity, be it trees, grass, wildlife, water or recreation, must be maintained in a continuously productive condition if it is to assist in maintaining high standards of living among the inhabitants of the region. Whenever the commodity is a biological product, a vulnerable point in the sustained yield cycle is that point separating one generation from the succeeding generation. As early as 1908, Henry Graves wrote, "The study of natural reproduction consitutes one of the most important lines of research of the American forester." If reproduction cannot be attained satisfactorily by natural means, some artificial, and frequently costly, method must be resorted to if

[1] Published as Scientific Journal Series Paper No. 2841 of the Minnesota Agricultural Experiment Station.

[2] The writer wishes to acknowledge his gratitude to Dr. Henry L. Hansen of the School of Forestry, and to Dr. Donald B. Lawrence of the Department of Botany at the University of Minnesota, both of whom provided advice and constructive criticism throughout the period of investigation. Sincere appreciation is expressed to

continuous productivity is to prevail. Recognizing the need for information relating to the influence of physical and biological factors of the environment upon the reproduction of particular species, forest ecologists have undertaken a number of studies since 1908. Nonetheless, for many important North American trees, but little information is yet available concerning the ecology of reproduction (Duncan 1952a).

Tamarack (*Larix laricina* (Du Roi) K. Koch) is one of the species, the reproductive characteristics of which, have been only superficially explored. It is one of the most widely ranging conifers in North America, extending from Newfoundland and Nova Scotia north and west to the valleys of the Koyukuk and the Yukon in Alaska. From the shores of the Beaufort Sea in northern MacKenzie and from northernmost Quebec where it frequently occurs on well-drained uplands, it extends south to the Atlantic coast of New Jersey, to western Maryland and northern West Virginia. In Minnesota, tamarack reaches its southwestern limit where, as elsewhere in the southern part of its range, it is generally confined to bog forests. Here, it survives in exceptionally hydric situations until, as the sites become more mesic, it is usually overtaken by more shade-tolerant arborescent species (Fig. 1). Where competition does not eliminate it and where favorable moisture conditions permit germination and early survival, however, it thrives on upland sites even in the southern part of its range (Fig. 2). On such favorable sites, it is without doubt the fastest growing conifer in the east (Cheyney 1942).

Ecologically, tamarack plays a significant role. It is a pioneer which, with few exceptions in the Lake States, initiates forest succession on bog lands often following immediately the sedge mat or the sphagnum stages (Conway 1949, Cooper 1913) and in other areas following the bog shrub stage (Cooper 1913, Gates 1942). Although frequently occurring in mixture with black spruce (*Picea mariana* (Mill.) B.S.P.) or northern white-cedar (*Thuja occidentalis* L.) tamarack is usually the first to appear and marks the initial change to the forest condition. It is the tree which prepares the way for other, and frequently more valuable, arborescent species although in so doing, it eventually brings about its own elimination.

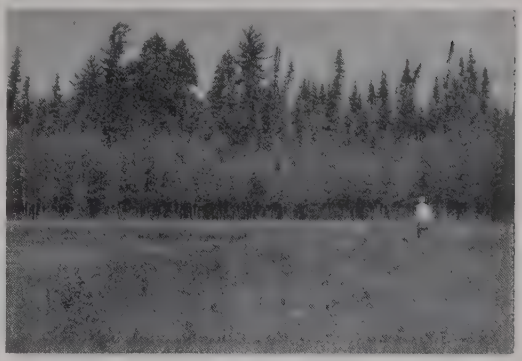

FIG. 1. Tamarack bordering a bog lake in Itasca State Park, Minnesota. At this particular location, the successional series is greatly compressed extending from the open lake through sedge mat, invading tamarack, black spruce, red pine, and white pine to balsam fir.

FIG. 2. Naturally seeded tamarack on sandy upland soil near Soderville, Minnesota. This is believed to have been a highway borrow pit on which tamarack seeded from adjacent bog-grown trees in a year of particularly favorable moisture conditions. No serious competition from more tolerant hardwoods has appeared on the site.

The present study was undertaken during the summers of 1948, 1949, and 1950 and most of the work was done at the Cloquet Experimental Forest, in the Itasca State Park region, and at Cedar Creek bog and nearby tamarack stands north of St. Paul. Some work was done elsewhere in tamarack stands scattered through various parts of Minnesota, from Ely and Big Falls to St. Cloud. The primary objective was to provide a background of information on some of the most important factors influencing natural reproduction in tamarack between the beginning of seed production and the end of the juvenile stage of seedling

Dr. F. H. Kaufert, Director of the School of Forestry, who made the studies possible, to Dr. T. Schantz-Hansen for making available the facilities of the Cloquet Experimental Forest and the Itasca Biological Station, to Dr. Ralph Hossfeld for suggestions in connection with some of the experimental apparatus, and to Professor R. M. Brown for advice on the statistical analyses used, and for permitting the writer to use the facilities of the Itasca Forestry Station. Acknowledgment is also made to other members of the staff of the University of Minnesota and the personnel of the Lake States Forest Experiment Station from whom advice was sought and whose suggestions were freely given, as well as to the members of the Minnesota State Division of Forestry and the United States Forest Service who helped to locate suitable field areas.

development. Much remains to be done. Only a few, if any, of the factors affecting reproduction have been thoroughly enough analyzed to obviate the need for further investigation. Information obtained, however, does provide a background against which silvicultural practices aimed at obtaining natural regeneration may be planned (Duncan 1952b).

The Seed

Methods

Cone production was studied by an ocular method using binoculars. The number of cones produced on a single typical branch of at least four levels in each tree was counted, the number of branches at each of these levels was ascertained, and through multiplication, the approximate total production for the entire tree was estimated. To find the number of seeds produced per cone, 10 cones from each of eight trees of ages varying from 30 to 60 years, were examined and the number and condition of the seed recorded. This was also done for all (23) of the cones produced on two 15- or 16-year-old trees.

Quantity of seed disseminated in the Cloquet Forest was ascertained by seed trap (Fig. 3) studies during the fall of 1948. Twelve one-quarter milacre traps were spread through seven pure and mixed tamarack stands. In addition, 12 traps were placed around a single isolated 35-foot tamarack tree during the fall of 1948 at Cloquet in a study of distance and direction of seed dissemination. Three traps were placed in each of the four cardinal compass directions at distances of one, two, and three times tree height from the base of the tree.

To ascertain the significance of rodents as an agent destructive of tamarack seed following dissemination, rodent exclosures covered with half-inch mesh hardware cloth were constructed and placed in the Cloquet Forest adjacent to seed trap locations.

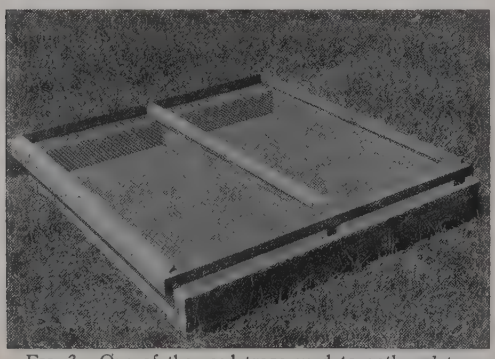

Fig. 3. One of the seed traps used to gather data on seed dissemination. It is divided in half to provide some check on uniformity of distribution and covers exactly one-quarter milacre. Rodents are excluded by half-inch mesh hardware cloth which covers the trap. The bottom is of 1/16 inch mesh screen wire.

Results and conclusions

Seed production.—Larix is monecious. Solitary staminate strobili are borne terminally on dwarf branches from leafless scaly buds. The buds from which they are produced, are recognizable in some species by the end of October by their greater size (Doyle 1918). When mature, the strobili are globose to sub-globose or oblong bodies. Ovulate strobili are small, red or, less commonly, greenish cones which attain nearly mature size in six to eight weeks. They are erect, more or less oblong in shape with nearly orbicular scales and light-colored bracts extending into elongated green tips. Strobili of both sexes appear with the leaves in late March, April, or early May in Minnesota tamarack. At St. Paul between 1941 and 1950, the foliage of tamarack first appeared between March 23 and April 24, averaging April 12 (Hodson 1951). The color of unripe cones is consistent for any one tree year after year, but varies among trees from dark red to light green. Between about the first and the middle of August in Minnesota, the cone scales dry out and begin to turn brown.

Good seed years for tamarack occur at five- to six-year intervals according to the U. S. Forest Service (1948). On the basis of the present limited study, good seed years occur in Minnesota at intervals of about four years. Baldwin (1942) suggests that one method of studying periodicity in seed production is "by studying the distribution of age classes in natural, undisturbed forest." Although this may have value for some species, it cannot be used satisfactorily for bog-grown tamarack. While good seed years are essential, of course, for good crops of seedlings, rodents may severely reduce seed supplies after they reach the ground. Furthermore, fluctuating water levels so seriously affect seedling survival that much of the evidence for abundant crops may be obliterated or at least greatly obscured.

Tamarack cones are small by comparison with those of most Lake States conifers. The number of seeds per mature cone varied from about 15 to as many as 48. The average number of seeds in cones taken from mature trees was 26 (26.24 ± 0.50) and none had more than 40. In two young trees, cut at 15 and 16 years of age, 28 to 48 seeds were found with an average of 39 (39.34 ± 0.36) per cone.

Although about 85 per cent of the seeds' pro-

duced by very young trees were well-developed, in mature trees about one-third are not filled. The largest seeds are borne on scales in the central half of the cone. The next lower scales also may produce some large seeds but the much smaller basal scales contain mostly unfilled seeds. Most of the terminal scales of the cone contain small undeveloped seeds, few of which are viable.

The number of cones borne on a particular tamarack tree is influenced primarily by the crown development which in turn is influenced by the competition provided by surrounding trees. After surveying the literature, Nelson (1950) concluded that light is generally considered a very important factor in seed production in conifers, particularly for intolerant species. Its importance to at least one intolerant species is borne out in the present study. Open-grown tamaracks of medium age (50 to 150 years) having large vigorous crowns were usually most productive and bore as many as 20,000 cones in a good seed year (Fig. 4). The heaviest seed-producing tree observed was open-grown and about 85 years of age but was only about 30 feet tall, having had the top broken out of it several years previously. Aside from the missing leader, it had a well-developed crown and was estimated to bear over 20,000 cones. At an average figure of 17 well-developed seeds per cone, such trees may produce over 300,000 good seeds in a single season. Many trees produce over 50,000 in a good year.

Tamarack begins seed production relatively early in life when in a favorable situation. Vigorous isolated bog trees begin to produce in Minnesota at about 15 years of age. Upland tamarack may produce cones as early as the twelfth or thirteenth year. The seed produced on such young tamarack appears to be as viable as that produced on older trees, the number of seeds per cone may be high (about 40) and the per cent of underdeveloped seed may be low (15 per cent). Trees grown under conditions of severe competition in well-stocked stands, however, may not produce seed crops until they have attained ages of 35 to 40 years. This lends support to Mayr's (1925) statement that trees grown in dense stands blossom at a later age than those grown in open stands, a difference which he estimates to average 20 years. Extremely old trees, up to about 250 years, may still produce cones even in light seed years. The limited evidence available on such trees indicates that after about 150 years tamaracks do not produce heavy crops. This is probably the result of crown deterioration which often begins at about this age.

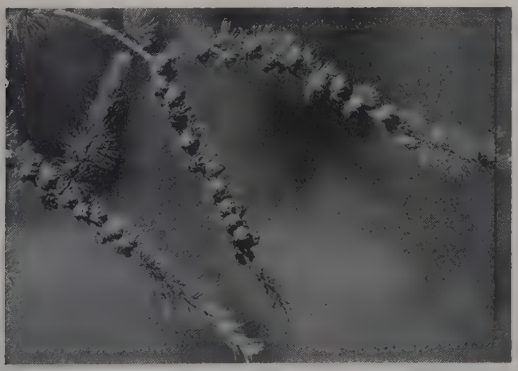

FIG. 4. In good seed years, many branches on open grown trees bear heavy cone crops like this one. In "bumper" years, most branches on such trees produce this sort of crop.

In well-stocked tamarack stands, the dominant and codominant trees produce most of the seeds, the intermediate, oppressed and suppressed bearing few or no cones. In a blowdown of tamarack at Cedar Creek, scattered standing trees having the best top development had the best cone crops. In the same area, many of the trees which were classified as intermediates bore cones, but very few suppressed trees carried any. In an adjacent stand unaffected by the storm, the dominants with much of the crown exposed produced good cone crops whereas suppressed trees bore no cones at all. A larger proportion of the intermediate and suppressed trees in the blowdown area bore cones than trees of comparable crown development in the adjacent stand.

Cones may appear on twigs of various ages but most frequently are borne on two-, three-, or four-year-old wood. On very young trees just coming into production, a few cones may appear on one-year-old wood, that is on wood of the preceding year's formation, although more commonly, they are found on two-year-old wood. On older trees, wood of from five to ten or even more years of age may produce cones. The location of the cones may be dependent, at least in part, upon the available light. Where growth is vigorous, the cones are most frequently found on recent wood (three years old or less). Where growth is very slow, cones are found on older wood. Old cones may be retained up to about five years before falling from the twig.

Seed destruction before dissemination.—Prior to ripening and dissemination, the seeds of tamarack may be destroyed in the cone. Several insects, including an aphid and at least two species of Dipteran larvae (Cecidomiidae), have been found in the cones. Insofar as could be ascertained, these feed on the succulent cone scales, however, and do not damage the seed directly. There is one species, a Lepidopteran larva belonging either to the

Olethreutidae or to the Tortricidae (Tripp 1951), which does seriously reduce the number of sound seeds produced on certain trees, up to 80 per cent of the cones being infested on some. These larvae feed on the seeds directly leaving simply the empty hull behind. While in few trees were more than five or six seeds eaten in any of the cones examined, these seeds were invariably among the largest and best developed. By the end of the season, this insect had destroyed half the good seeds in three-fourths of the cones on one tree examined. In some years, at least on some trees, therefore, it may become a serious factor in reducing seed supply.

Squirrels and birds may cause some loss of seeds prior to maturity. The red squirrel (*Tamiasciurus hudsonicus* Erxleben) frequently has been observed cutting cone-bearing twigs from tamaracks before the cones were matured. These are then usually carried to caches. They have also been observed feeding on seeds in the cones well into the winter at Cedar Creek bog (Lawrence 1951). The American red crossbill (*Loxia curvirostra pusilla* Gloger) and doubtless other seed-eating birds, occasionally feed on tamarack seeds. However, neither rodents nor birds are believed to be very significant factors in seed destruction before disemination.

Seed dissemination.—In Minnesota, tamarack seeds may begin to be disseminated about three months after pollination, between late August and mid-September, varying with the location and the season. At Cloquet in 1948, seed traps studies revealed that the first seeds fell on September 1. Within the first 20 days of the season (*i.e.,* before September 20) about 65 per cent of the 3409 seed collected had been disseminated; an additional 25 per cent were disseminated within the second 20 days (before October 10); during the next 20 days (before October 31) about 7½ per cent of the total were released; the remaining 2½ per cent fell during the winter (before mid-June when final counts were made). Although a larger number fell during the overwinter period than the 2½ per cent indicated, cutting tests showed that less than 6 per cent of the number released during that time could possibly be viable. These only were included.

The heaviest concentration of seeds disseminated at Cloquet were under more or less open stands where the mature tamaracks were fairly good-sized (four to 10 inches DBH) and had well-developed thrifty crowns. Here the number distributed varied from about 1,500,000 to nearly 2,500,000 per acre in 1948, which was a good seed year. In a moderately heavy, 80-year-old stand of tamarack where crowns were much smaller and less vigorous, the dissemination varied from 500,000 to about 1,200,000 per acre during the same year. In a "bumper" crop year, the evidence, based on seedlings found in the spring of 1948 at Itasca, indicates a probable production of five million or more filled seeds per acre in a medium stocked stand. By comparison with other conifers (Anonymous 1950, Bates 1923, Chapman 1926, Cox 1911, Eyre and LeBarron 1944, Fowells 1944, Haig *et al.* 1941, Isaac 1943, Jemison and Korstian 1944, LeBarron 1948, Lowdermilk 1925, and Shirley 1941) tamarack is a prolific seed producer.

The distance of dissemination of quantities of seed satisfactory for good stocking of regeneration is small. Heavy seedling stands may be secured up to a distance about equal to the height of the seed trees, fair stands are found up to twice the tree height distant, and a few scattered seedlings may be found at greater ranges. In the seed-trap study around an isolated tree bearing a heavy seed crop, 458 seeds were collected in the quarter milacre trap immediately beneath the tree. About 10 per cent of that number of seeds was found per equivalent area at a distance equal to the tree's height, about four per cent at twice the tree's height, and less than two per cent at a distance equal to three times the tree's height. Since this tree was open-grown, the distance of dissemination because of unobstructed winds, was undoubtedly appreciably greater than would occur from the edge of a tamarack stand.

Seed destruction following dissemination.—Following dissemination, the consumption of seeds by rodents may be a significant factor in reducing the number present to germinate satisfactorily (Table I). This appears to be particularly true if the seeds are exposed on mineral soil where they can

TABLE I. *Number of seedlings appearing per quarter milacre plot beneath exclosure and on adjacent area without rodent protection*

Plot	With exclosure	No exclosure
Litter, duff plots	40	8
	36	20
	0	0
	20	9
	0	3
	76	44
	28	17
	16	7
	40	20
Total on litter, duff plots	256	128
Sphagnum plot	104	21
Mineral soil plot	58	14
Total on all plots	418	163

be more readily located than in the litter and duff. Comparison of germination on areas under rodent exclosures during the winter with adjacent areas of equal size without protection, reveals four times as many seedlings established on protected mineral soil as on the unprotected area. Under litter and duff which was undisturbed, seedlings were twice as numerous where protected as where rodent protection was not provided. This difference is highly significant. On *Sphagnum,* where the effect of the rodent exclosure was to compress the moss and reduce its growth rate, a five to one increase in tamarack germination resulted. Reduction of rodent losses was partially responsible, but probably more important was the improvement of seedbed conditions otherwise. The increase parallels observations made by Roe (1949) with respect to black spruce germination on compressed *Sphagnum.*

Although the species of rodents concerned with seed destruction are not definitely known, the red-backed vole (*Clethrionomys gapperi gapperi* Vigors), the white-footed mouse (*Peromyscus leucopus novaboracensis* Fisher), and the shrews (*Sorex articus laricorum* Jackson and *Sorex cinereus* Kerr.) may be important destructive species. These are common in boggy areas and on bog periphery in Minnesota (Gunderson 1950, Marshall 1951). Both *Clethrionomys* and *Peromyscus* are known to feed heavily on seeds (Burt 1946). Moore (1942) has shown that in coastal Oregon Douglas fir, shrews eat not only insects but frequently coniferous tree seed and may be a factor accounting for the dominance of small-seeded species in some areas. Tamarack, being a small-seeded species, is probably less seriously affected by rodents than some of the larger-seeded species with which it is sometimes associated, such as balsam fir.

There is also evidence that between November 1 and mid-June, some seeds may be destroyed by bacterial or fungus attack. Of the seed collected in traps during the overwintering period, some had decayed by the time of collection in June. Since these were in the seed traps during the overwintering period, and consequently were exposed to unnatural conditions, it is not necessarily a good measure of the amount of decay which could be expected in the litter or duff. However, this may be a significant factor in seed loss following dissemination in the fall, at least in certain years and under conditions favorable to the destructive organisms. Baker (1950) believes "these (microbial) losses are not important among sound, uninjured seeds." Rathbun-Gravatt (1931) has shown that for pine at least, decay of unruptured seed may be caused by damping-off fungi, but that this is less serious than the destruction of radicles after they have emerged but before the seedling breaks through the soil.

Germination

Methods

In several of the field investigations concerned with germination, the objective was to determine the range within which certain environmental factors operate; in others, where variables could be reduced, an effort was made to determine the influence of certain factors on germination under field conditions. The germination factors which were studied in the field include temperature, moisture, oxygen supply, ground cover, and hydrogen-ion concentration. In the laboratory, germination studies were concerned not only with these factors but also with light, tree age at the time of seed production, and time of seed dissemination.

Seeds from two sources were used for the laboratory tests and in those field tests where seeds were sown artificially. One of these collections was made on the Superior National Forest in Minnesota on August 27 and 28, 1940. Following drying and extraction, the seeds were stored at 5° C. in a wax-sealed pint jar from October 11, 1940 until March 4, 1948 at which time they were stratified in moist sand at 5° C. prior to tests made that spring. The second source was collected on the Cloquet Experimental Forest on September 4, 1948. Following extraction, the seeds were placed in cold storage at 5° C. in a wax-sealed pint jar where they remained until removed for stratification.

Surface-soil temperature determinations in the field were made using a glass immersion-type thermometer which was inserted into the surface half-inch of the germinating medium.

In the laboratory, temperature tests were conducted in a refrigerated room which was maintained at 5° C. in order to provide the lower temperatures desired in the test. The apparatus (Fig. 5) included a thermostatic control device for each set of temperature conditions and heating elements for each sand flat. The laboratory test with a 7° C. variation from high to low temperature levels was conducted using seeds from the Superior National Forest. The remaining laboratory temperature tests were conducted using the seeds from the Cloquet Experimental Forest.

Each sand flat in which testing was being undertaken was subjected to alternations of thermostatic settings at 12-hour intervals. The higher temperatures were attained by heating of the coils

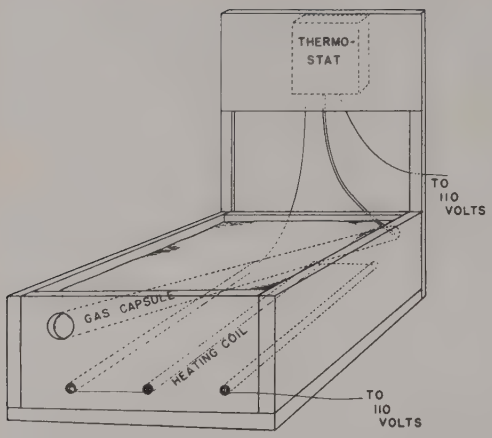

FIG. 5. This 12-inch by 6-inch seed flat is equipped with a Minneapolis Honeywell T 415 A temperature controller. The regulator may be set to maintain the temperature within 1° C of the amount provided for in the thermostat setting. The heating coil circuit consists of three nickel-chrome alloy wire coils inserted in glass tubing. A thermometer installed at seed level was used in each flat to check the accuracy of the thermostatic control.

in the flats, the lower temperatures by allowing the 5° C. room temperature to bring the flats down to the lower level established by the thermostats. The heating coils were placed 2½ inches below the sand surface and the seeds were covered to a depth of about ¼ inch. Each flat was covered with a sheet of glass to minimize evaporational losses and tap water was added at two- or three-day intervals providing plenty of moisture so that this factor would not reduce germination. The sand flats were constructed of wood and ready drainage was provided.

The influence of light upon germination was studied using seeds from the Superior National Forest collection. After a 63-day stratification period, the seeds were removed on May 7 and about 185 were placed in petri dishes on filter paper for each of five light levels. The light was supplied for 14 hours daily by three 150-watt tungsten lamps and two 100-watt fluorescent daylight lamps suspended 22 inches and 16½ inches respectively above a table. All petri dishes were rotated each day from one position to the next on the table. Temperatures were alternated between about 21° C. or 22° C. during the dark period to 28° C. or 29° C. during the light period. No replications were made. Light was varied from an intensity of approximately 850 foot candles (about one-tenth of full sunlight) by using an unshaded dish, to total darkness; three intermediate levels were obtained by shading with varying numbers of layers of cheesecloth. Photoelectric cell measurements showed these intermediate intensities to be about 340, 160, and 115 foot candles.

In both germination and seedling survival studies, it was necessary to ascertain the moisture level of the surface material of the forest floor. Craib (1929) has pointed out that "moisture expressed as a percentage of dry soil weight is a relative quantity, the significance of which is dependent upon soil density." The moisture equivalent is not too satisfactory a measure of moisture content for organic soils such as were characteristic in this study because of great variability from sample to sample. As early as 1864, Schumacher suggested the desirability of working with soils in place when determining the physical properties, particularly their water relations. In the present study, per cent moisture by volume shows much less fluctuation at the wilting point of tamarack seedlings than does per cent based on dry weight.

Moisture determinations were made using two standard circular soil cans, one inch deep and three inches in diameter with a content of 112 cubic centimeters, for each quarter milacre plot. These were pressed into the surface material to full depth, and were removed including all of the surface material above the level of the rim of the inverted can. The tops were replaced and the can and contents were weighed. After oven-drying for 24 hours at 100° C. to 105° C., they were reweighed. Results were expressed as a per cent by volume and as a per cent by weight. The former was found to be much more consistent than the latter for determining critical levels of moisture when a variety of germinating media, from mineral soil through humus to sphagnum, were being tested. Neither measure was found to be entirely satisfactory for all media.

Results and conclusions

General.—For tamarack, the relationship between number of seedlings emerging from the seedbed and number of seeds disseminated on it varies widely extending from zero per cent to as high as 75 per cent or even more under near optimum laboratory conditions. The point within this range at which field germination actually lies varies with many factors of the environment of which moisture level, oxygen supply, and rodent populations are among the most important. Temperature is seldom, if ever, directly limiting although it does affect speed of germination which may be a significant factor in later survival of the seedlings.

Laboratory tests on fresh, unselected, sound tamarack seeds indicated germination capacities

under favorable temperature and moisture conditions varying from 30 to 60 per cent. A summary of germination data from various sources (U.S.F.S. 1948) for this species indicates that germinative capacity may vary from 10 to 85 per cent with an average of 47 per cent. In the field, however, when germination is expressed on the basis of number of seeds disseminated, these high percentages are not attained. In the spring of 1949 at Cloquet, slightly less than 5 per cent of the seed, all of which were naturally disseminated and none of which were provided rodent protection, germinated successfully. At Cedar Creek in the spring of 1950, artificially seeded fall-sown plots in those situations where at least some germination occurred, showed a 4 per cent average. On a few plots where moisture was definitely limiting, no germination took place. These figures are to be compared with a 44 per cent over-all field germination for jack pine (*Pinus banksiana*

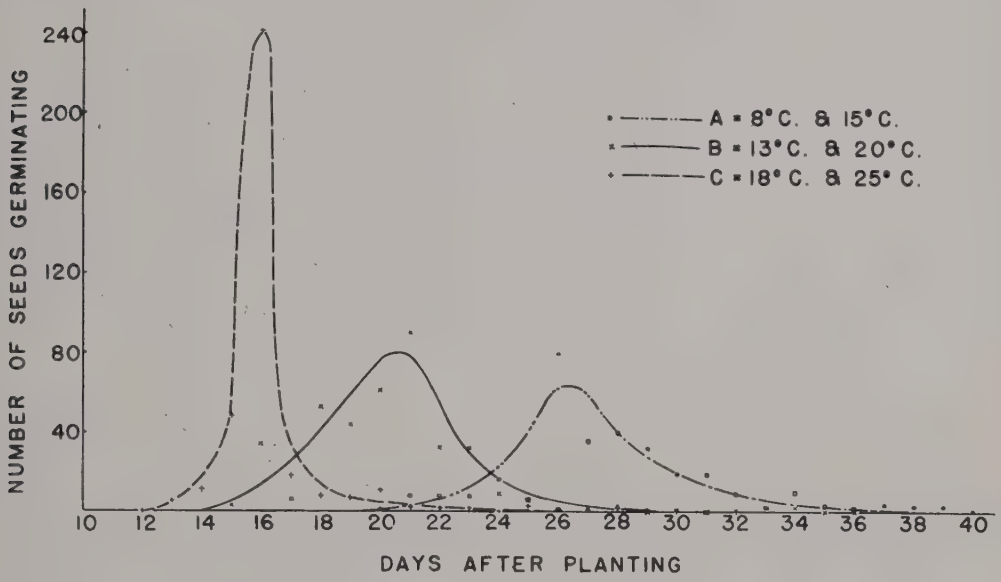

FIG. 7. Daily germination under various temperature conditions (see Table II, 2nd test). The test was begun on May 22, and 400 seeds were used in each of the five flats.

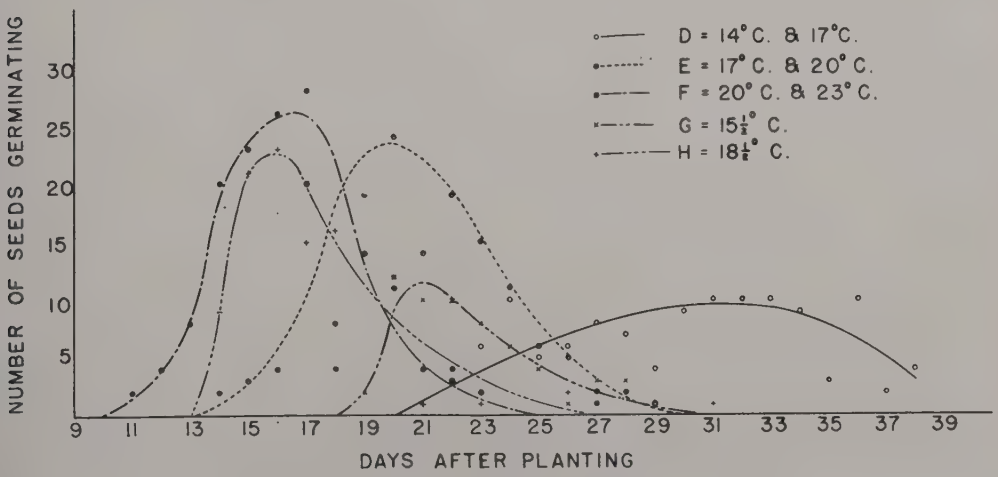

FIG. 6. Daily germination under various temperature conditions (see Table II, 1st test). The test was begun on May 18, and 800 seeds were used in each of the three flats.

Lamb.) and 26 per cent for black spruce (LeBarron 1944).

Temperature influence.—Under normal conditions, the surface soil in tamarack bogs during the germination period varies from a low of about 10° C. to about 20° C., although higher temperatures up to 28° C., are not infrequently found when the sites are exposed to full sunlight. In the springs of 1948 and 1949, germination generally reached its peak when the surface soils had attained temperatures of 17° C. to 19° C. during the day. However, on sites in deep white-cedar shade, germination occurred at lower temperatures (13° C. to 14° C.: on the more exposed sites, on the other hand, it began at higher temperatures (21° C. to 22° C.). Germination on unshaded sites began earlier (about May 23 to 30 at Cedar Creek and about June 5 to 10 at Cloquet) than on the shaded sites where it began considerably later (about June 8 to 15 at Cedar Creek and June 15 to 25 at Cloquet). These differences in time of germination are undoubtedly the result of temperature differences. White-cedar seeds in the shaded situation (at Cedar Creek) germinated about a week to 10 days earlier than the tamarack.

Field investigations also indicated that seed germination on the sites where higher temperatures prevailed had a much more concentrated germination period than on sites where it remained lower. Under a heavy stand of white-cedar where surface soil temperatures never were recorded as exceeding 19° C., seeds were still germinating as late as August 1. In the warmer, more exposed sites, on the other hand, all germinating seeds emerged before late June.

To determine more precisely the influence of temperature on germination in tamarack, an experiment was designed to test the effects in the laboratory. Since fluctuating temperatures are normal in the natural seedbed, these were used in preference to constant temperatures. Investigations of surface soil temperature variations under natural conditions revealed that daily fluctuations, while quite variable ranging from less than 1° C. to over 10° C., averaged about 3° C. These findings were used as guides in the laboratory tem-

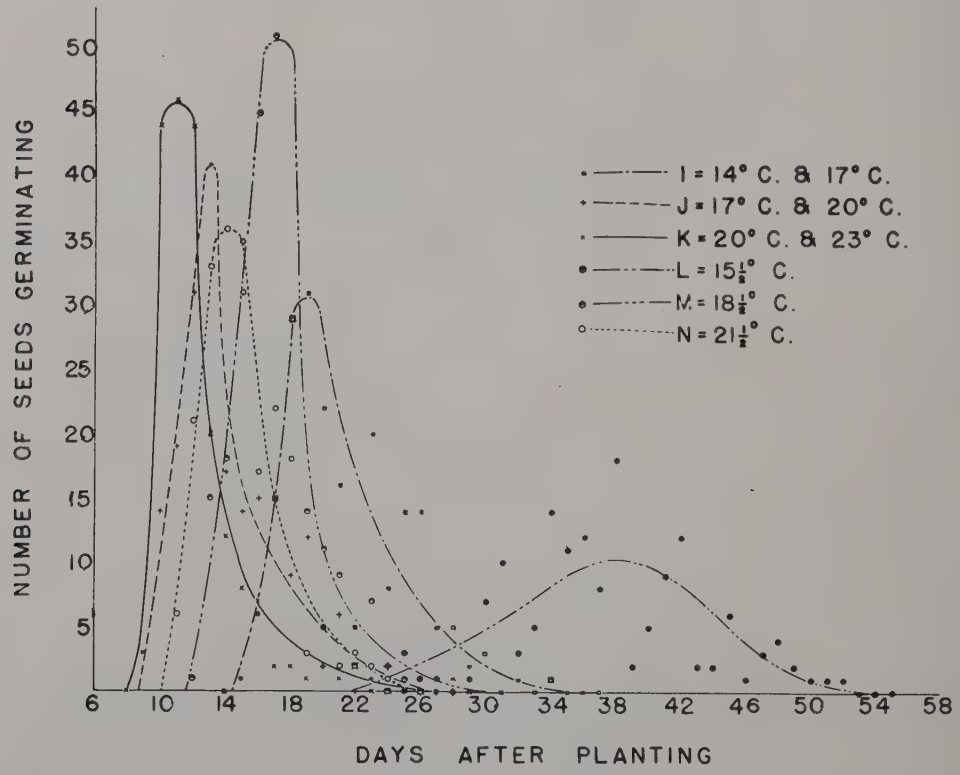

FIG. 8. Daily germination under various temperature conditions (see Table II, 3rd test). The test was begun on August 2, and 400 seeds were used in each of the six flats.

TABLE II. *Summary of germination data secured in laboratory temperature tests*

1st Test (1948)
Seed source - Superior National Forest
800 seeds in each flat
75-day stratification period
Test started May 18

Test	Temp. range	Germ. cap. %	Peak day	°Days at peak
A.....	8° C and 15° C	38.5+	26	206
B.....	13° C and 20° C	45.2	21	252
C.....	18° C and 25° C	45.4	16	278

2nd Test (1950)
Seed source - Cloquet Experimental Forest
400 seeds in each flat
70-day stratification period
Test started May 22

Test	Temp. range	Germ. cap. %	Peak day	°Days at peak
D....	14° C and 17° C	30.0+	32-33	360
E.....	17° C and 20° C	37.7	20	285
F.....	20° C and 23° C	38.7	16	269
G....	15½° C	14.7	21	245
H....	18½° C	27.0	16	212

3rd Test (1950)
Seed source - Cloquet Experimental Forest
400 seeds in each flat
53-day stratification period
Test started August 2

Test	Temp. range	Germ. cap. %	Peak day	°Days at peak
I.....	14° C and 17° C	49.5	19	222
J.....	17° C and 20° C	49.5	13	157
K....	20° C and 23° C	49.5	11	159
L.....	15½° C	36.7	38	434
M....	18½° C	59.7	17	226
N....	21½° C	48.5	14	234

perature tests. The results of the tests are shown graphically in Figures 6, 7, and 8 and are summarized in Table II.

The laboratory temperature tests when combined with observations made in the field, lead to certain conclusions as well as to additional questions needing further investigation. The generalizations which appear to be most valid and at the same time to have the most significance follow. (1) Total seed germination probably is not influenced appreciably by temperature variations found in the natural environment. All sites not under water, where field records were maintained, had attained temperatures for the top half-inch of seedbed of at least 17° C. on several occasions before mid-July. The laboratory tests indicate that given enough time and favorable moisture conditions, fluctuating temperatures with a high range of only 15° C. to 17° C. may be expected to provide as good total germination as temperatures with a maximum up to 25° C. Temperatures in Minnesota tamarack bogs do not attain such high levels that total germination is reduced because of temperature effect alone. Seldom do natural seedbed temperatures exceed 25° C. which is not limiting. (2) Maximum germination rate may be expected to be relatively early on unshaded sites and may be relatively late in shaded areas. In some years, this is very important in that it may become a limiting factor in subsequent survival. Those seedlings starting late may not obtain sufficient depth of root penetration to survive summer drought. (3) Germination on unshaded sites may be expected to be more concentrated than in shaded locations. Instead of requiring 10 days or even longer for most (75 per cent) of the viable seed to germinate, the same precentage of germination may be secured within a four-day to five-day period. This also usually will help to contribute toward higher ultimate survival of the seedlings.

Some additional interesting relationships may be obtained from the data. With the exception of one test which gave an unaccountably high total (Fig. 8, M), higher germination capacities were attained at alternating temperatures than at constant temperature in tamarack. This appears to be true whether the constant level is an average between the two alternating levels or is at the higher of the two alternating levels. Davis (1939), the U.S.F.S. (1948), and others have found maximum germinative capacity under alternating temperatures for many species. In other plants constant temperatures are satisfactory (Harrington 1921).

Since it is possible that peak germination or a given per cent of germination of a particular lot of seed occurs when a certain number of degree days has been attained, this was computed for all ranges (Table II). The results indicate that simple temperature summation above physiological zero (assumed to be 4° C.) does not provide a consistently maintained point at which germination may be expected to take place. The data are very inconsistent and additional experimental work is required to determine what factors influence the amount of heat necessary for germination.

The effect of moisture and oxygen supply.— Moisture is essential, of course, for satisfactory germination and may be limiting when deficient. No satisfactory laboratory experimental study was undertaken to determine what level is required for germination. Probably moisture is seldom limiting during winter months when seed in the duff is

undergoing after-ripening. Under these conditions, low temperature will prevent germination. In spring, when the temperature has risen to a satisfactory point, moisture content of the seed may have dropped to a level which is limiting.

Field evidence obtained at Cedar Creek bog in the spring of 1948 indicated that moisture deficiency may sometimes be limiting insofar as germination in tamarack is concerned. Here, seed soaked for five days in cold water before being placed in the field, germinated between zero per cent and five per cent at various locations on the surface of relatively dry sandy soils. In moist, bog situations in the same general area, on the other hand, germination in similar tests varied from seven per cent to 35 per cent. Rudolf (1950) has concluded tentatively, however, that 14 days of cold soaking is necessary in tamarack and that seven days is insufficient to obtain good response in germination. The five-day treatment, therefore, probably did not provide as good a test as is desirable. Also rodent protection was not provided, and mice or shrews may have been an important limiting factor on the mineral soil plots.

In the spring of 1950 in the Cedar Creek area, similar results were again recorded with fall-planted seeds. On sites where leaf litter was fairly heavy and moisture was limited as well as on dry mineral soils, no germination took place on four plots of 100 seeds each. On sites more favorable from the standpoint of moisture availability, the germination on six plots of 100 seeds each averaged four per cent (from one to nine per cent).

Undisturbed plots adjacent to the seed-trap collections of the fall and winter of 1948-49 at Cloquet, were classified on the basis of moisture determinations made at the height of germination during the middle of June 1949. The precipitation records at Cloquet from the 15th of May to the June samplings reveal about 1.3 inches, or a 30 per cent deficiency, below normal for the period. All plots where moisture content of the surface inch of material was less than 12 per cent by volume were classified arbitrarily as dry sites (Table III). One such plot showed no germination. Five plots with moisture levels between 12 and 22 per cent in the surface inch were classified as intermediate with respect to moisture content and showed an average germination of nearly 4.1 per cent. The remaining six plots with moisture content in the surface inch between 22 and 32 per cent by volume were considered moist sites and showed successful germination of 7.5 per cent of the seeds which fell on them. There is a nearly straight line relationship between germination and moisture content within the limits of these data. Correlation analysis between moisture content of the germination medium at the time of germination and the per cent of seed germinating gives a correlation (r) of .503. These data as well as laboratory experience indicate that higher moisture levels than those found, probably would have produced higher germination, although under conditions of flooding, germination will again drop to zero.

TABLE III. *The relationship of germination to moisture content of the germination medium on 11 quarter milacre plots adjacent to seed traps of equal size. Spring, 1949. Cloquet Experimental Forest*

Moisture level*	Total seeds disseminated (on adjacent traps)	Number of seeds germinating	Per cent germinating
10½.....	468	0	0.0
15.....	354	13	3.7
15.....	124	8	6.5
16.....	227	9	4.0
16½.....	34	3	8.8
21.....	581	21	3.6
23½.....	454	20	4.4
24½.....	324	44	13.6
25.....	211	9	4.3
30.....	53	8	15.1
31½.....	108	5	4.6

Summarized results

Moisture level*	Number of plots	Seeds dis-seminated	Number of seeds germinating	Per cent germinating
2 - 12....	1	468	0	0.0
12 - 22....	5	1,320	54	4.1
22 - 32....	5	1,150	86	7.5

*Expressed as per cent by volume based on two determinations made at height of germination period in mid-June.

Cooley (1903) in a study of tamarack reproduction in Maine, where annual precipitation exceeded 45 inches and where fogs were common, found abundant reproduction on open mineral soil. She writes, "the best places for germination are those cleared fields open to the sun and covered with low, thin grasses. . . ." Germination on such areas in Minnesota can be expected only in years of particularly favorable moisture conditions and on sites where rodent populations are not high.

A shortage of oxygen resulting from flooding is not infrequently limiting for tamarack. Although some seeds germinate satisfactorily under water (Morinaga 1926), on the basis of both field and laboratory evidence seeds of tamarack do not so long as kept submerged, even though temperature conditions may be favorable. In this respect they resemble the seeds of bald cypress (*Taxodium distichum* (L.) Richard), another intolerant swamp conifer (Demaree 1933). Other factors being

favorable, within one to three weeks following release from submersion, some tamarack seeds germinated even though they had been submerged in warm stagnant water in the greenhouse at St. Paul for a period of one month or more. There is some field evidence to indicate that the germination following flooding may be less than would have occurred had the flooding not taken place, but this needs controlled experimental study for verification. Baker (1950) suggests that seeds soaked in water swell, the seedcoat may crack and then decay will set in. This may account for reduced germination following release from flooding in tamarack.

Light as an influence.—Although light has been found to affect the germination of a number of species (Nelson 1940, Nelson 1950, Haack 1906), a test of the effect of varying light intensity upon the germination of tamarack seeds following thorough after-ripening and at near optimum temperatures, shows no correlation. The results presented in tabular and graphical form (Table IV and Fig. 9) indicate no consistent trend relating light levels to germination per cent.

The effect of pH level.—Determination of hydrogen-ion concentrations was made in most of the tamarack bogs which were intensively studied. These varied from generally acid bogs at Cloquet (pH 4.5 to pH 6.2) to circumneutral bogs at Itasca (pH 6.9 to pH 7.6). In all of these bogs, enough seeds germinated in good years to provide good seedling stands. Averell and McGrew (1929) found the average pH on tamarack sites in northern Minnesota to be 5.6. Wherry (1922) indicates that tamarack tolerates an "unusually wide" pH range but classifies it as "preferring circumneutral habitats." Baldwin (1942) writes, "the influence of acidity on germination is mostly indirect. . . . In spite of the divergent opinions and theories on the influence of acidity on germination, there is a considerable body of evidence pointing to a favorable effect of mildly acid reactions on seed. . . ." Oosting (1948) believes that "Under ordinary conditions, the hydrogen-ions themselves probably have little direct effect upon plants. . . ." It seems probable that pH is seldom if ever a limiting factor insofar as germination of tamarack seeds is concerned.

TABLE IV. *Germination under five different light conditions during 15-day period in May*

	Quantity of light (foot-candles)				
	850	340	160	115	dark-ness
Total seeds germinating....	147	160	135	162	133
Seed in test.....	192	192	177	200	171
Germination %...	76½	83½	76½	81	78

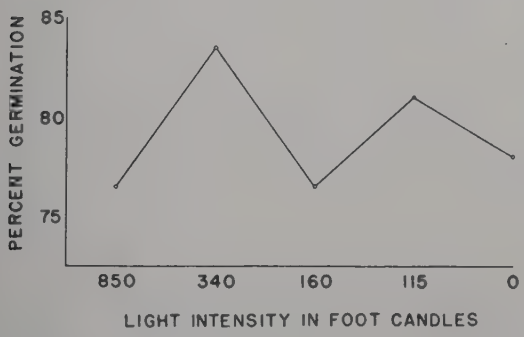

FIG. 9. Effect of various light intensities on seed germination.

The influence of ground cover and germination medium.—The microclimate of the seed is determined, at least in part, by the surrounding ground cover which directly influences the amount of sunlight penetrating to the seed's immediate environment. This affects the temperature which in turn indirectly affects the rate of evaporation of moisture available to the seed. Furthermore, the competing ground cover, by consuming moisture, reduces the amount available for germination. Some types of ground cover permit more rapid evaporation from the seed bed than do others which retain moisture to a greater degree. These variations, along with others may materially change the physical factors of the environment, thereby directly affecting germination.

Beneath existing tamarack stands in Minnesota, the ground cover is frequently composed largely of a variety of mosses. Several species of *Sphagnum, Mnium,* and *Plagiothecium* are common as are *Aulocomnium palustre* (W. and M.) Schw., *Calliergon cordifolium* (Hedw.) Kindb., *Drepanocladus vernicosis* (Lindb.) Warnst., *Helodium blandowii* (W. and M.) Warnst., and *Thuidium delicatulum* (Hedw.) Hitt. Various species of the sedges belonging to the genus *Carex,* particularly *C. lasiocarpa* Ehrh., a relic of the sedge mat stage, *C. trisperma* Dew., C. *leptalea* Wahlenb., and *C. lacustris* Willd., may be fairly abundant. In some tamarack stands, a number of herbaceous plants are also found including *Maianthemum canadense* Desf., *Caltha palustris* L., *Coptis groenlandica* (Oeder) Fern., *Sarracenia purpurea* L., *Mitella nuda* L., *Potentilla palustris* (L.) Scop., *Viola* spp., *Pyrola rotundifolia* L., *Lysimachia thyrsiflora* L., *Menyanthes trifoliata* L., *Galium* spp., *Linnaea borealis* L., and others. Common shrubs include *Salix pedicellaris* Pursh var. *hypo-*

glauca Fern., *Betula pumila* L. var. *glandulifera* Regel, *Alnus rugosa* (Du Roi) Spreng., *Rubus pubescens* Raf., *Cornus stolonifera* Michx., *Ledum groenlandicum* Oeder, *Chamaedaphne calyculata* (L.) Moench, and *Vaccinium oxycoccus* L., among the more important. Other areas in which tamarack seeds were found germinating were covered with a thin litter beneath which lay raw humus. Most frequently in existing stands, needle litter was interspersed with mosses and occasional sedge, herbaceous or shrubby plants.

More seedlings were found on fine moss (primarily *Mnium, Drepanocladus,* and *Helodium*) than elsewhere. In one stand in the Itasca area during the early summer of 1948 a study was made of 41 randomly selected plots, each one square link in size (one-millionth acre). Of these, 10 were low lying and wet, with a cover of *Mnium* and carried a total of three, or 0.3 newly germinated seedlings per plot (later when more oxygen was available with a receding water table, additional seedlings appeared), seven were at an intermediate elevation covered with *Sphagnum* and carried seven seedlings, or one per plot, seven were at a similar level covered with *Helodium blandowii, Calliergon cordifolium,* and *Thuidium delicatulum* and had 69 seedlings, or 9.9 per plot, eight were at a somewhat higher level covered with needles or humus and occasional *Mnium affine* Bland., with 87 new seedlings, or 10.9 per plot, and nine were *Carex* knolls which stood several inches above the general ground level having 13 seedlings, or 1.4 per plot.

Adjacent to the 12 seed traps used at Cloquet during the seed dissemination period of 1948-49, 11 per cent of the seed disseminated germinated on non-Sphagnum moss cover. This was over twice the germination secured on *Sphagnum* (4½ per cent), sedge plots (4 per cent), needle litter plots (1½ per cent), or mineral soil when not protected by a rodent exclosure (4 per cent). The bare mineral soil provided better germination (14½ per cent) than a non-Sphagnum moss cover if rodent losses were eliminated. However, there is likewise a correlation here with moisture level which is probably a determining factor for type of vegetative cover as well as for tamarack seed germination. Most of the ground-covering non-Sphagnum mosses appear to be good indicators, at least in existing tamarack stands, of moisture conditions suitable for satisfactory seed germination.

Sphagnum, although it is probably a good medium for germination because of frequent favorable moisture and temperature conditions near its basal portion, is not satisfactory in the long run because it competes with the growing seedlings for light and because it dries out later in the season. Germination data collected, using it as a medium, are probably lower than actuality, because of the difficulty of locating sprouting seedlings in *Sphagnum.* This is particularly true in vigorously growing *Sphagnum* beds. If the growth rate of the *Sphagnum* is reduced, and particularly if the moss mat is compressed, it may prove to be an ideal germination medium. Schantz-Hansen (1931) also found this true for black spruce.

Age of cone-producing tree as an influence.—Seeds collected from cones of 15- and 16-year-old trees were tested for germinative capacity for comparison with the seed produced by trees 40 years of age and older. Two hundred seeds from each of two young trees gave tests of 27.5 per cent and 31 per cent as compared with seed-trap collections made the same season and treated in exactly the same way following collection, in which 2,663 seeds gave an average germination of 31.2 per cent.

Insofar as seed viability is concerned, therefore, it appears that young trees could be expected to reproduce about as satisfactorily as older trees. However, while the number of seeds produced per cone is relatively high in young trees, the total number of cones borne is very small and older trees with larger crowns are much more satisfactory for regenerative purposes.

The influence of date of dissemination.—Seeds collected from the seed traps during the fall of 1948 at Cloquet were divided into two groups: (1) those disseminated prior to October 11, and (2) those which fell on that date or later. Only seeds which superficially appeared to be sound and filled were used in the test, all cracked, rotting, and obviously unfilled seed having been eliminated. A pronounced difference in total germination was found, those seeds which were disseminated early giving a germination of about 37 per cent compared with one of about 20 per cent for seed disseminated late in the season (Table V). The t test applied to these data indicates a highly significant difference. These differences are not unexpected, particularly when one considers that the best developed seeds are found in the central part of the cone which is the first to open. Seed borne in the basal and terminal scales are frequently unfilled and those which are filled are usually of smaller than average size.

Retention of seed viability in the duff.—Naturally disseminated tamarack seeds ordinarily germinate the spring following dissemination. The field evidence for this statement, however, needs experimental verification. Under only two of the 12 seed traps put out in the fall of 1948 at Cloquet, did any seedlings appear following removal

TABLE V. *Differences in germination resulting from tests of seed disseminated prior to October 11 compared with those disseminated October 11 or later at the Cloquet Experimental Forest, fall and winter, 1948*

Early disseminated seeds			Late disseminated seeds		
Seeds sown	Germinated	Per cent germination	Seeds sown	Germinated	Per cent germination
35	12	34.5	50	9	18
80	28	35	30	1	3.5
300	47	15.5	40	4	10
30	14	46.5	18	3	16.5
100	42	42	100	23	23
200	68	34	150	41	27.5
200	69	34.5	150	27	18
300	110	36.5	125	41	30.5
135	59	43.5	150	19	12.5
12	8	66.5	18	3	16.5
200	131	65.5	50	17	34
125	52	44	55	4	7
1,717	640	37.3	946	192	20.3

TABLE VI. *Germination in Itasca State Park area in the spring of 1948 as compared with the spring of 1949 on quarter milacre plots*

Plot number	1948 seedlings	1949 seedlings	Plot number	1948 seedlings	1949 seedlings
1.....	159	1	7.....	88	0
2.....	276	4	10.....	12	0
3.....	15	5	11.....	151+	2
5.....	135	3	12.....	39+	0
6.....	104	2			
			Totals...	979+	17

the next spring. The three found on these trap locations may have been from seeds which reached the ground surface by accident during collection from the traps. Still better evidence is provided by the failure of an appreciable number of seedlings to appear on the Itasca plots during the spring of 1949, the second spring following the very heavy seed crop of 1947. The seed crop in 1948, although very small by comparison with that of 1947, was large enough ao provide some reproduction. In spite of this, the first year seedlings found on the Itasca plots in the spring of 1949 were less than two per cent of the number found in the spring of 1948 (Table VI). This ratio is probably not far from the cone-crop ratio of the two years.

THE SEEDLING

Methods

The plots used throughout the seedling investigations in this study were one-quarter milacre in size. Such a plot measures five links, 39.6 inches, or 1.006 meters on each side. Larger plots could not be inspected thoroughly enough to find small seedlings when first germinated without destroying them, particularly where ground cover was heavy or where seedlings were very abundant. All seedlings on each study plot were marked using small wooden medical applicators 6½ inches long. Where necessary to distinguish several different classifications of seedlings on one plot, the tips of the applicators were painted using various colors.

Inasmuch as it was not possible to visit all plots at frequent intervals, a large proportion of the loss of seedlings on the various plots could not be assigned satisfactorily to a definite cause. As a matter of fact, only about 10 per cent of the loss was assigned specifically. Certain assumptions could have been made on many of the others based on circumstantial evidence, but such uncertain evidence has been excluded from the data.

In an effort to determine the direct influence of light upon seedling survival, a series of shade frames (Fig. 10) were constructed and placed over third-year seedlings in the Iron Springs bog just north of Itasca State Park. This bog is spring-fed and well-drained. The shade frames were four feet square and were designed to satisfactorily shade the entire quarter milacre plot. Screen wire of one to three layers, heavy muslin, and a combination of the muslin and screen wire tacked to the frames, provided shade in varying degrees.

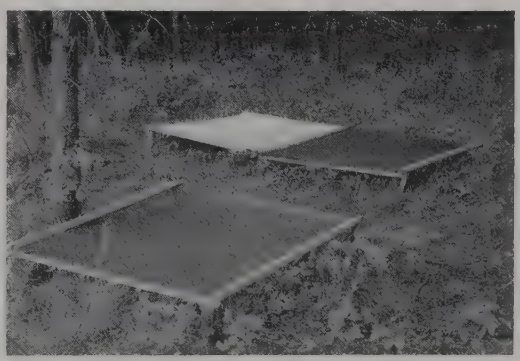

FIG. 10. Three of the four-foot square shade frames used in the light intensity study undertaken at Iron Springs bog at Itasca State Park. Heavy muslin or varying numbers of layers of screen or both, were used to provide shade.

The frames were placed over the eight plots at a height of approximately eight inches on June 23. Light intensity was ascertained using a model B Norwood Director incident light exposure meter. Four readings were taken beneath the shade frame

on each plot, as well as on the five control plots on 12 occasions representing various dates, times of day, and sky conditions through the summer. At the same time, seedling counts were made, and the cause of mortality, when it could be assigned, was recorded. The frames were removed September 26.

Results and conclusions

General.—The early seedling stage is probably the most critical time in the establishment of a stand of tamarack. Mortality during the first three years under severe conditions may reduce a stand of half a millon new seedlings per acre to only scattered individuals incapable of providing reasonable stocking. The following Itasca data have shown that losses during the first three years following a good seed year may be extremely high. Of 1,630 new seedlings on nine plots, about 30 per cent survived the first summer. Of those alive at the end of the first summer, half survived the following winter; by the end of the second growing season, the survival based on original germination was only six per cent. Of those still living at the end of the second summer 70 per cent survived the winter; during the third summer, survival for the year was reduced to about 60 per cent. Thus, of the original 1,630 new seedlings on the plots, only 53 or about 3½ per cent lived to the end of the third growing season.

Survival at the end of the third summer varies widely with individual bogs. At Iron Springs, where water levels are very constant in a well-drained, spring-fed area, survival at the end of the third summer was high, nearly 14 per cent of 571 original seedlings. On the LaSalle Trail plots, the 203 new seedlings had all died by the end of the second growing season. Since only about five per cent of the disseminated seeds germinate, it can be calculated that approximately 32,000 seeds were probably distributed over all the Itasca plots. On this basis one seed in 1,600 resulted in a surviving seedling at the end of the third summer.

Douglas fir seedling survival, as shown in a study made by Isaac (1938) of the 1928 crop in western Washington, averaged about 17 per cent at the end of 1930. The 1929 crop had a survival of five per cent three years later. At the end of the third growing season in this species, survival was from 1½ to five times that found in tamarack. In the investigations by Haig, *et al.* (1941) in the northern Idaho region, western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), which is comparable to tamarack in seed size, showed a survival of about 18 per cent of the original seedlings at the end of the third year. In the same study at the end of the three-year period, western white pine (*Pinus monticola* Dougl.) survival was 45 per cent. Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.) was 40 per cent, western larch (*Larix occidentalis,* Nutt.) was 39 per cent, grand fir (*Abies grandis* (Dougl.) Lind.) was 50 per cent, and western redcedar (*Thuja plicata* Donn.) was 40 per cent. In central Idaho on grazed areas, Sparhawk (1918) has shown that ponderosa pine (*Pinus ponderosa* Laws.) and Douglas fir seedlings have a survival at the end of the third year of about 7½ per cent. In the same study, lodgepole pine (*Pinus contorta* Dougl.) showed a survival of about 25 per cent at the end of the third year.

These comparisons with other species indicate that tamarack has more severe mortality during the first three years following germination than other conifers for which data are available. If reproduction is to be successful, the causes of this mortality must be analyzed and removed wherever possible in silvicultural practice.

Seedling survival in the succulent stage.—Baker (1950) distinguishes between two periods in the critical time of seedling establishment, first the succulent stage and later the juvenile stage. The first of these continues for from five to six weeks in tamarack grown beneath an overstory of older trees and is terminated by the hardening of the hypocotyl. Mortality during this stage was nearly 40 per cent of 705 seedlings studied on 52 plots at Itasca, Cloquet, and Cedar Creek. During this stage, over half of the dying seedlings for which cause of mortality could be assigned definitely showed symptoms of damping-off.

Davis, *et al.* (1938) describe four types of damping-off, "pre-emergence damping-off," "post-emergence damping-off," "root rot," and "top damping-off,"on which the only type definitely found in this study of tamarack was the second, post-emergence damping-off. This is typical of the succulent stage and is marked by characteristic constriction of the hypocotyl just above the germinating medium followed by toppling of the seedling. Neither sun scald nor wind injury symptoms (Hartley, *et al.* 1918), which are similar in general appearance, occurred among the seedlings on the sites studied. The specific organisms causing the damping-off, however, were not identified. There is very limited evidence to indicate that mortality from damping-off may be most severe in circum-neutral bogs and less serious on the acid sites. On the basis of knowledge common to forest nursery practice, this is to be expected.

It is not improbable that some loss, perhaps

considerable loss, in tamarack is the result of pre-emergence damping-off. Such losses may destroy two-thirds of the seedlings in coniferous nurseries in some years (Hartley, *et al.* 1918). Hartley (1921) has found a high correlation between the number of seedlings emerging and the percentage of subsequent loss resulting from ordinary damping-off for two species of western firs. In tamarack also, pre-emergence damping-off may account, in part, for the low germination characteristics of the species in the natural environment, since ordinary damping-off is a common cause of loss. However, damping-off mortality before the seedling appears above the ground was not analyzed in the present study.

Other important causes of loss found in the succulent stage are mechanical injury, drowning, and drought. Mechanical injury refers to trampling or breaking of the hypocotyl by animals including man. On the Itasca plots, such losses were sustained from man, deer, and porcupines and undoubtedly also from other mammals who chanced to walk over the plots.

On the basis of very limited evidence, it appears that young tamarack seedlings in the succulent stage cannot survive more than about a week of complete submergence under water. If only the roots are submerged, even succulent seedlings can withstand floods of one week's duration or longer.

On many of the plots, some seeds germinated after mid-July. Few of the resulting seedlings survived and by all odds the most important cause of mortality among them was drought. The depth of root penetration of tamarack seedlings in the succulent stage rarely exceeds three-quarters of an inch and particularly after the first of August, this surface layer may dry out almost completely.

An additional source of loss which proved to be of little importance on the plots included in the period of this study, was defoliation by insects including the larva of the larch sawfly (*Pristiphora erichsonii* (Hartig)). It seems probable, however, that in epidemic attacks of this insect when older trees are defoliated, the feeding larvae may fall to the ground and there consume all or most of the tamarack seedlings on the area.

Seedling survival in the juvenile stage.—The juvenile stage of seedling development begins with the hardening of the hypocotyl and continues for an indefinite period until the seedling may be considered established (Baker 1950). In tamarack, a particular seedling may be "established" in three years, or perhaps even in two, if it is grown in favorable conditions of soil, light, and moisture. On the other hand, tamarack seedlings grown under a well-stocked overstory of the same species will not become established, even in four or five years or more.

During this study in which many tamarack stands in various parts of Minnesota were inspected, only one seedling over four years of age was found in reasonably well-stocked stands. That lone seedling was five years old and died in its sixth year. Very few seedlings four years of age were found although a large population of three-year seedlings appearing after the bumper seed crop of 1947 survived to the end of the summer of 1950 in favorable areas at Itasca State Park. On the other hand, in many areas where the tamarack overstory was scattered or even where a fairly heavy cover of shrubs existed without a tamarack overstory, seedling tamarack of many ages were to be found and satisfactory stands were being established.

Light influence.—During the early succulent stage of development the tamarack seedling depends, at least in major part, upon food stored in the seed for sustenance. In the latter part of the succulent stage and following entrance upon the juvenile stage, however, when the seedling must manufacture its own food, light becomes the dominating or master factor. While light deficiency may not be a direct cause of death resulting from the seedling's inability to maintain its photosynthetic activity above the compensation point, it frequently is a contributing factor which weakens the seedling to causes of mortality not directly ascribable to light.

Light conditions within the tamarack stands intensively studied were quite variable because of stocking variations (Table VII). The lowest average intensities encountered in pure tamarack without an understory of shrubs were about 5½ per cent of full sunlight. These were found in mature heavy stands on good sites. Where black spruce or balsam fir were intermixed with tamarack, average intensities as low as three to 3½ per cent were encountered. In those stands which had an overstory sufficiently open to permit the entrance of alder or other shrubs, the ground level intensity was further decreased to a minimum of about 1½ per cent of that in the open. The well-stocked stands of pure tamarack having little or no shrubby understory usually have light intensities between six and 10 per cent whereas it is only the stands in which holes in the canopy are found that exceed 15 per cent.

The only study concerned with the compensation point of tamarack seedlings known to the writer is that of Burns (1923) in which seedlings were exposed to three hours of electric light and the results were reduced to an expression in terms

TABLE VII. *Summary of light intensities at seedling level in stands at Cloquet and Itasca between mid-June and mid-September. All intensities are expressed in foot-candles and were taken with a Norwood Director Model B incident light exposure meter*

Sky condition	Location	Full light intensity (in the open) average	Average intensity in all stands	Number of stands	Number of readings	Stand average as per cent of average in open			
						Range			
						Minimum		Maximum	Average
						Under-brush	No under-brush		
Clear	Itasca	8360	990	8	112	1	6½	29	13
	Cloquet	8510	1165	10	45	—	2½	21½	8
Cloudy	Itasca	3720	430	7	48	2½	5	20½	12
	Cloquet	2460	435	10	69	—	6	27½	16½
All days	Itasca	....	...	...	160	1½	6	26	13
	Cloquet	....	...	...	114	—	3½	23½	11

of full sunlight on the basis of total thermal energy. This work indicated that the compensation point in a test of seven, 18- to 24-inch tall, potted tamarack seedlings is 9.8 per cent of sunlight at noon on December 22 in Vermont. Converted to summer conditions in Minnesota, this is about five per cent of full sunlight. If these measurements are representative for tamarack seedlings of this type, such seedlings can successfully maintain photosynthesis above the compensation point in most, if not all, pure tamarack stands without an understory occurring in Minnesota. However, in the heavier stands there is little residual photosynthate, and even moderate injury probably will result in mortality.

Tolerance has been defined by the Society of American Foresters (1950) as "the capacity of a tree to develop and grow in the shade of, and in competition with, other trees." An alternative definition is also offered as follows: "a general term for the relative ability of a species to survive a deficiency of an essential growth requirement, such as light, moisture or nutrient supply." Shirley (1943) recommends that the term be used in the second sense and that the specific type of tolerance be stated when it is used, *i.e.*, shade tolerance, tolerance of low nitrogen supply, drought tolerance, etc. This provides a more precise usage than the first definition quoted and therefore is superior, at least for scientific purposes.

Tamarack is quite universally conceded to be a very intolerant species (Baker 1949), in the sense of the first definition given above. Cheyney (1942) under his discussion of the species with reference to its light requirements writes ". . . (it) is probably the most intolerant tree in the east."

Seedling tamaracks are able to withstand drought and flooding more satisfactorily if grown in good light conditions than where light intensity is low. Survival of drought is largely dependent upon the depth of rooting which in seedlings beyond the succulent stage appears to be dependent upon the amount of light received. Likewise, seedlings grown under full sunlight appear to be better able to withstand flooding than seedlings grown in light intensities of only 10 to 20 per cent of full light. These relationships will be discussed in greater detail under the sections dealing with drought and flooding.

A study of the influence of light upon third-year seedling survival was undertaken at Iron Springs bog just north of Itasca State Park. Light intensity readings on the plots, the type of cover used, survival percentages, and other pertinent data are shown in Table VIII. Survival plotted over light intensity is also shown in graphical form (Fig. 11). These data indicate a pronounced drop in survival at an intensity of 200 to 300 foot-candles, which is a little over two or three per cent of the intensity of full sunlight on bright, clear days during the summer in Minnesota. However, there is some question as to the precise cause of this sudden downward trend in the curve. Since the four plots having lowest survival are the plots covered with muslin, these are the plots on which humidity was increased by reduced air movement and rate of evaporation. If these plots are eliminated there is still a general downward trend with decreasing light intensity but no sharp descent at the 200 foot-candle level.

The shade frame plots were intentionally located in an area where water levels were relatively constant. Therefore drought mortality as well as

TABLE VIII. *Summary of data gathered on 13 plots at different levels of light intensity at Iron Springs bog, showing average, maximum, and minimum light intensities and seedling survival for each.*

Average light intensity*	Maximum intensity* (average of four readings)	Minimum intensity* (average of four readings)	Number of light observations	Seedlings present on June 23	Seedlings present on Sept 26	Per cent survival	Type of cover
1120	2960	335	48	29	28	97	1 screen
968	1000	405	48	21	19	90	control
849	2430	440	40	90	82	91	control
790	1845	250	48	29	22	76	control
775	2660	170	48	17	14	82	control
569	1075	305	36	14	14	100	control
426	1275	90	48	35	30	86	2 screens
377	945	85	48	22	18	82	2 screens
244	740	20	48	25	9	41	1 muslin, 1 screen
130	410	50	48	25	19	76	4 screens
101	230	55	40	87	42	48	1 muslin
62	190	25	40	46	29	63	1 muslin
41	125	15	48	28	5	18	1 muslin, 1 screen

*In foot-candles.

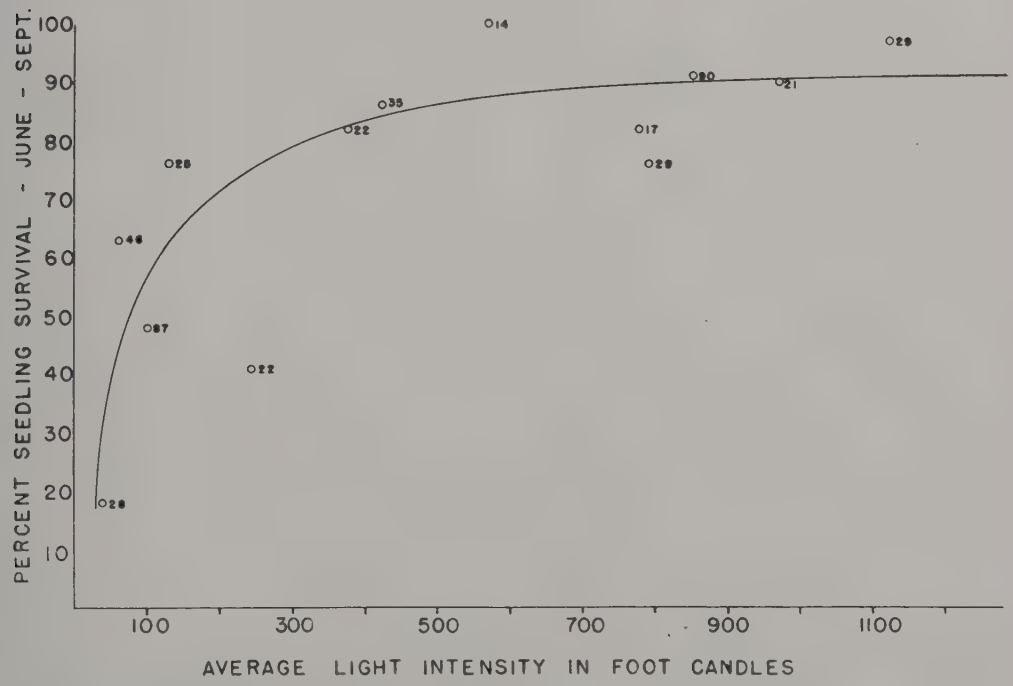

FIG. 11. Survival of third-year tamarack seedlings from June 23 to September 26 under various light intensities at Iron Springs bog, Itasca State Park. Numbers beside points indicate number of seedlings present at the beginning of the period for each intensity.

flood losses were eliminated, leaving insects and damping-off as the major causes of mortality. The two most important causes of death in third-year seedlings had been eliminated but the importance of damping-off was increased. Bates (1925), in studying a variety of first-year coniferous seedlings, also found an increase in damping-off losses with a decrease in light intensity. In his study, instead of using shading and natural light, artificial light was used, its intensity being determined by the distance of the seedlings from the source. Damping-off was an important cause of loss among those seedlings farthest from the light even on sand which had been "peculiarly free" of damping-off when well-insolated.

The amount of mortality resulting directly from

light reduction over a three-month period beginning at the end of June is probably less serious than a similar reduction for the entire year. Wiesner (1907) has pointed out that for all forest species, the minimum light requirement is relatively high at the time of bursting of the buds. For European larch (*Larix decidua* Mill.), he found this starting minimum for foliage to be half of full light. Decreased light early in the season, therefore, may be most significant to seedling survival in tamarack. Being a deciduous species, however, the shading beneath a tamarack overstory is much less severe than shading beneath an overstory of other conifers. One might expect appreciably higher mortality of tamarack seedlings beneath an overstory including black spruce or white-cedar, for example, than beneath a stand of pure tamarack.

Shirley (1935) points out that although failure of some forest species to succeed themselves is frequently attributed to failure to grow in the reduced light intensity, probably more precisely the major difference between shade tolerants and intolerants is the length of time which they can survive light intensities too low for growth. Tamarack seedlings appear to be able to survive from three to six years under an overstory of the same species. The shading test undertaken in this study on third-year seedlings for only three months extends over too short a period to provide conclusive data. Additional erperimental study is required to determine the significance of light as a direct factor in seedling survival. Certainly as a contributing factor, it is of great importance as will be shown.

The effect of drought.—A major cause of mortality among first-year seedlings after they have passed the succulent stage and a cause of considerable importance among older juveniles is moisture deficiency. Even bog species, such as tamarack, are subject to serious losses from drought. As has been pointed out in previous discussion, germination occurs only on sites where moisture levels are above about 12 per cent by volume. Under moisture conditions above 22 per cent but short of saturation, appreciably better germination may be expected. Occasionally, because of flooding, the most satisfactory germination occurs on the higher portions of a particular area, on knolls several inches above the general bog level. In late summer, these dry out most readily and in some years it may be found that the sites on which germination was most successful are those on which seedling mortality is highest.

Many writers (Livingston and Koketsu 1920, Conrad and Veihmeyer 1929) have pointed out that plant survival under drought conditions depends upon ability to push new absorbing root surfaces into regions where moisture has not been exhausted. The rapid exhaustion of moisture in the immediate vicinity of seedling rootlets both by absorption and by surface evaporation, and the inability of capillary action to replace it at a rate fast enough to meet plant needs, frequently renders good growing conditions, particularly with respect to light, essential to survival. This has been very well demonstrated by Haig (1936) in his study of mortality of seedlings of western white pine and associated species. Western larch, in this study, showed 93 per cent drought mortality among residual seedlings in full shade plots but only two per cent and four per cent in part-shade and full-sun conditions respectively. After averaging mortality among all of the species studied, Haig found the lowest rate, five per cent, occurred among residual seedlings in partial shade. In full sunlight where dry, hot conditions prevailed, rapid and deep seedling root penetration kept drought mortality to 16 per cent. In full shade, where shallow surface soil drying was accompanied by shallow root penetration, drought mortality rose to 61 per cent average for all species studied.

Superficial evaporation of the moisture from the forest floor is a major factor in the survival of first-year tamarack seedlings and also of older seedlings grown in shaded situations. The loss of moisture at greater depths resulting from tree root competition is of little or no significance at least in the juvenile stage of tamarack development. It may be of some significance later on, although even then, in the bog environment usually occupied by this species in Minnesota, deep competition is of less significance than for many upland species. Except in prolonged drought periods, water tables probably rarely recede beneath the reach of mature root systems. This has been found true for swamp-grown black spruce (Shirley 1934). Probably the major reason that seedling mortality is lower on *Mnium*-covered sites, for instance, than on litter-occupied areas is the higher level of moisture retained during critical periods in the surface soil beneath the moss.

The rate of root development in tamarack is slow, in part because it grows from small seeds, and the stored food available to the seedling for rapid root elongation is very limited. Of the first-year seedlings inspected in a series of examinations of individuals removed from older tamarack stands in the latter part of the first summer, none had root systems penetrating to a depth exceeding 1½ inches and the average was less than one inch. The tops of such seedlings were usually longer than their roots. Western larch seedlings grown in full shade had a minimum root penetration of

0.5 inch and a maximum of 1.8 inches in late August. In full sunlight, corresponding figures were 6.1 inches and 13.4 inches, respectively (Haig 1936).

The moisture content of the surface inch of the forest floor was measured in the present study with special reference to the ability of first-year tamarack seedlings to survive late summer droughts. Variations through the season on the several sites studied ranged from two per cent to over 60 per cent by volume or from about 30 per cent to over 1200 per cent by weight in bog soils. The highest moisture contents appear in the very light mosses such as *Sphagnum* where tamarack seeds sometimes germinate. With few exceptions, moisture levels during the first two to 2½ months of the summer were satisfactory for seedling growth, ranging from 15 to 35 per cent by volume. During late August and September in many years, however, the levels may be expected to drop appreciably to ranges between 10 and 25 per cent by volume, or during critical periods, even lower. On the basis of limited field evidence it appears that shade-grown first-year tamarack seedlings during late August or early September drought periods, fail to survive moisture contents by volume in the surface inch of material below eight to nine per cent. In the humus soils typical beneath tamarack stands, this level is about 100 to 110 per cent by weight. On mineral soil (loamy sand) plots, shade-grown tamarack seedlings in their first year showed no drought mortality when moisture content by volume descended to 13 per cent which was about 11 per cent by weight.

Three-year-old seedlings because of deeper root penetration frequently exceeding three inches, can withstand reductions of moisture levels in the surface inch of material to about four per cent by volume or from 45 to 65 per cent by weight in organic soils. This level was never reached on the plots studied in the field except upon sites so dry that no tamarack seeds germinated on the area in the first place. It was attained in greenhouse flats where samples of the forest floor including tamarack seedlings were removed for study.

Additional experimental evidence obtained from seedling studies in the greenhouse indicates that first-year seedlings produced in full sunlight in organic soils brought in from tamarack bogs also will survive moisture level in the surface inch down to three to four per cent by volume. Such seedlings have a much lower top-root ratio than do seedlings of equal age grown in the shade of a tamarack overstory. While the root length of such seedlings is not quite as great as that of shade-grown three-year-old seedlings, it does approach them more closely than might be expected (Fig. 12).

FIG. 12. At left, four three-year-old tamarack seedlings grown in the shade of an overstory at Iron Springs bog. In center, four one-year-old seedlings grown in full sunlight on bog soil. At right, four one-year-old seedlings grown in full sunlight on sand. The root systems in these one-year-old seedlings are nearly as well-developed as those of the three-year-old shade-grown seedlings.

Hofmann (1918), in a study of western larch on four areas in northern Idaho, found 22 per cent seedling establishment in the shade and 70 per cent in the open. In a study involving eight coniferous species, Bates (1925) concludes that root development suffers most severely from light deficiency, predisposing the seedlings to mortality from drought and nutrient deficiency.

In sterile sand, where because of nutrient deficiency, the first-year full-sun seedling roots are less well-developed than in the organic soils (Fig. 12) but still much better developed than those of forest-grown seedlings on organic soils, much lower levels of moisture in the surface material can be sustained. General mortality occurs only when the surface inch drops to a moisture level of less than one per cent by volume. Presumably, the difference between this medium and organic soils is the result of tighter packing of the mineral soil about the seedling root system and a smaller percentage at hygroscopic water, thereby rendering more of the moisture present available to the seedling.

The effect of flooding.—During the summer of 1949, extremely heavy rainfall in July caused a mid-summer flooding of some of the bogs being studied both at Cloquet and at Itasca. The inundation of many of the plots under observation caused heavy mortality among seedlings in the juvenile stage. In this respect tamarack resembles bald cypress (Demaree 1933) in that neither conifer, even though both are frequently found in aquatic environments, can withstand flooding of much duration as seedlings. Flooding is not uncommon in tamarack stands.

The field evidence from the Cloquet Forest indicates that first-year seedlings grown beneath existing stands will be killed by complete submergence for a period of approximately one week to 10 days. Partial submergence covering about half

of the top with complete submergence of the roots for a similar period of time may or may not kill similar seedlings immediately. By the end of the summer, however, most seedlings so covered die. Submergence of only the roots for this period results in little, if any, mortality. At Itasca second-year shade-grown seedlings subjected to complete submergence for about three weeks all died. The submerged portions of similar seedlings partially inundated for the same period on these plots turned brown. By the end of the summer all such seedlings were also dead.

To obtain additional verification of the influence of flooding upon seedlings, sections of the forest floor containing three-year-old seedlings were transplanted in August of 1950 from the Iron Springs area at Itasca to the St. Paul greenhouse where they were subjected to flooding for a period of three weeks (Table IX). Also, first-year seedlings grown in full sunlight in the greenhouse on the same soils were subjected to a similar test for a four-week period (Table X). The results indicate that, as was true in the drought tests, three-year-old seedlings grown in the shade of older tamarack stands are no better able to withstand severe conditions than are one-year-old seedlings grown in full sunlight. Seedlings grown in full light appear to be much more capable of withstanding flooding than do seedlings of the same age grown in the shade of a tamarack overstory.

Miscellaneous influences.—Fire may be a factor in regeneration. Cutover tamarack stands examined in the course of the study had occasionally been broadcast-burned to reduce the slash following cutting. These were still completely barren of tree reproduction several years later. Light fires burning through existing stands, on the other hand, actually encouraged natural reproduction by reducing the overstory and by reducing the severity of ground competitors. In two stands examined which recently had been burned lightly, moist pockets had not been charred, and in these pockets first-year tamarack seedlings showed vigorous growth. Many of the trees in the overstory as well as the shrub cover beneath had been partially or completely killed. On an adjacent area with a more or less complete overstory and a heavy shrub cover of *Ledum*, not a single surviving seedling was found.

Most tamarack seedlings beyond the succulent stage have ectotrophic mycorrhizae. In one stand examined at Itasca, some first-year seedlings had mycorrhizal roots whereas others did not. No noticeable differences in the thrift of the two classes of seedlings was found.

Browsing has not been found on tamarack seedlings in the present study and appears to be a factor of little or no importance at the present time in the areas studied. DeBoer (1947), in a survey of deer damage to forest reproduction in heavily browsed forest areas in Wisconsin, found comparatively little injury in tamarack. Some injury by snowshoe hares was recorded in his study in addition to limited deer damage.

TABLE IX. *Effect of three weeks' flooding on tamarack seedlings transplanted from the floor of a tamarack stand in August of their third year to the greenhouse. Condition determined two weeks after removal from flooding*

Condition	Degree of submergence			Control (not flooded)
	Complete	Part of top	Roots only	
Good	2	24	10	22
Unhealthy	3	3	5	2
Dead	50	6	0	1

TABLE X. *Effect of four weeks' flooding on first-year tamarack seedlings grown in organic soil in the greenhouse. Condition determined two weeks after removal from flooding*

Condition	Complete submergence	Control (not flooded)
Good	4	50
Unhealthy	1	0
Dead	91	5

VEGETATIVE REPRODUCTION

Layering as a means of regeneration among conifers is not uncommon, particularly in the genera *Picea* and *Abies* (Cooper 1911). Mayr (1925) indicates that *Larix* also reproduces by this method. Cooper points out that layering occurs more frequently with increasing latitude and altitude. The findings in Minnesota relative to layering in tamarack, therefore, may be conservative since the region lies at the southwestern limit of its range. This form of reproduction may be more common toward its northern limits.

Throughout the study seedling tamaracks were found to produce roots quite readily along the stem as *Sphagnum* covered the lower portion. However, only one tree definitely produced by layering was found in the course of this study. This was in an open bog containing a heavy growth of *Chamaedaphne* and of *Sphagnum*. The rapid-growing *Sphagnum* had completely covered the lower portion of the scattered black spruces and tamaracks. Many small spruce trees obviously had originated by layering, forming groups around the older trees in the center. Similar arrangement of tamaracks in groups was not found. The evidence supports the presumption usually made, that

at least in Minnesota, vegetative reproduction in tamarack is of no significance.

The Reproductive Ecology Having Silivicultural Implications

If tamarack is to be managed successfully on a sustained yield basis, the practicing forester must recognize and give due consideration to its ecological characteristics, particularly with respect to natural regeneration. The biology of any species determines the framework within which economic management must operate.

As has been indicated, tamarack is very intolerant of shade, perhaps as much so as any tree native to the region. Even the seedlings are seriously affected by light deficiency. The species, however, is relatively tolerant of root submergence. These two characteristics result in its confinement primarily to wet lands in the southern part of its range where it cannot compete with the large variety of semi-tolerant or tolerant species characteristic on the uplands. On the bog lands, however, competition is limited to a few species. At the northward extensions of its range, on the other hand, where competing species are less abundant, it appears on the upland. Even in the southernmost portions of its range, this may occur if competition is very limited and if moisture conditions are suitable for germination. In any part of its range, the first essential to satisfactory regeneration is abundant light.

Tamarack differs from bald cypress in the juvenile stages. In that species, Mattoon (1916) has shown that the seeds and seedlings demand a very high degree of soil moisture for satisfactory development. He believes that in cypress, the confinement of the species to swamps may result not only from inability to compete on better sites but that the necessities for satisfactory reproduction, principally a super-abundant water supply, are also involved. Tamarack appears not to be limited to bogs because of exceptionally high moisture requirements during the reproductive stage although germination may be restricted by early season drought.

Satisfactory regeneration, however, has been shown to involve a relatively constant water level. Both drought and flooding are serious causes of mortality among seedlings and in spite of the fact that provision of abundant light will help to reduce loss from these causes, it will not eliminate them. The control of water levels is frequently impossible. However, successful steps have been taken by foresters in Europe and more recently in the United States to increase growth rate in existing stands through drainage (Averell and McGrew 1929, Hoene 1951, LeBarron and Neetzel 1942, and others). It is possible that at least in some areas, a limited amount of effort directed toward maintenance of consistent water levels could be economically justified to attain natural reproduction of tamarack.

The third major requirement for successful tamarack regeneration is a satisfactory seed source. If the stand of reproduction is to be well-stocked, vigorous trees of seed-bearing age (preferably 50 to 150 years) having well-developed crowns must be found within one to two times their height of all portions of the area to be stocked. Fulfillment of these requirements—abundant light, reasonably consistent water levels, and a satisfactory seed source—will usually assure natural tamarack regeneration.

One additional consideration, attention to which will help to relieve the environmental resistance faced by tamarack in the reproductive process, is the reduction of rodent populations. Such action may be necessary only on certain areas where, and in particular years when, populations are high. Even with peak rodent populations, however, it is possible that in heavy seed years on bog soils where the small seeds of tamarack are not easily found, a satisfactory stand may be established.

Summary

Tamarack (*Larix laricina*), a native conifer widely distributed in North America, has received but little attention with respect to its ecological characteristics. During the summers of 1948, 1949, and 1950, studies undertaken in Minnesota were directed toward a determination of some of the more important factors affecting its reproduction.

Good seed crops, which occurred at intervals of about four years in greatest abundance on 50- to 150-year-old trees with well-developed crowns, produced one to two million filled seeds per acre in stands of medium stocking. Most of the good seeds were disseminated during September and October and satisfactory regeneration was seldom secured beyond two tree-heights distant from the source. Seed destruction may be caused in significant quantities before dissemination by a seed-eating Lepidopteran larva and after dissemination by various rodents which may be particularly destructive on bare mineral soil surfaces.

Field germination in tamarack was low by comparison with seed-flat germination tests, averaging only four or five per cent. On exposed sites where temperatures were relatively high, germination started earlier and was more concentrated than on shaded sites, although total germination did not vary between them because of temperature differences. Tamarack seeds will not germinate under

water and prolonged spring flooding may result in reduced germination. Moisture deficiency frequently limited field germination, and considerable improvement was recorded with increasing moisture content from about 10 to 35 per cent by volume of the germination medium. Under a fine moss cover (*i.e., Mnium, Helodium,* and *Drepanocladus*), maximum field germination in existing stands was secured, although compressed *Sphagnum* and mineral soil protected from rodents gave better results. Light did not influence germination nor does pH appear to be a seriously limiting factor since tamarack occurs on sites ranging at least from pH 4.5 to pH 7.5. Young trees bore seeds which germinated as well as those from older trees. There was a highly significant decrease in germination among seeds collected after mid-October when compared with those collected earlier. Viable seeds did not lay over in the duff to the second year in appreciable quantities if at all.

Only about 3½ per cent of new tamarack seedlings survived to the end of the third summer, a very low percentage when compared with other North American conifers for which data are available. During the succulent stage of seedling development which lasts for from five to six weeks, damping-off was the principal cause of mortality, although mechanical injury, drought, drowning, and insects also reduced survival. In the juvenile stage immediately following, light deficiency, drought and drowning were major causes of loss. No seedlings surviving beyond the sixth year were found in well-stocked, existing stands during the course of the study.

Light intensities in pure tamarack stands, lacking a shrub understory, varied from about 5½ per cent to more than 25 per cent of full light in the open. Lower intensities occur where black spruce or balsam fir are in mixture or where a shrubby understory exists. Damping-off, drought losses, and flooding mortality may be expected to increase with reductions in light intensity, particularly at the lower levels. First-year, forest-grown seedlings, with a root penetration averaging only about an inch, did not survive moisture contents in the surface inch below about nine per cent by volume. Seedlings of equal age grown in full light as well as three-year-old forest-grown seedlings, both of which may have root penetrations of 2½ to 3½ inches, withstood reductions to about four per cent. Complete or partial top submergence by flooding for a week or more killed first-year, forest-grown seedlings which were beyond the succulent stage. First-year seedlings grown in full sunlight and shade-grown three-year-old seedlings showed 90 per cent or greater mortality following three to four weeks of submersion.

Severe fires appear to completely eliminate tamarack regeneration for many years but light burning may be beneficial by reducing competition for light. Most tamarack seedlings had mycorrhizal roots but first-year seedlings lacking mycorrhizae were not retarded. Browsing by mammals as a cause of loss in tamarack was of minor importance.

Although reproduction by layering does occur in tamarack, it is so uncommon as to be of little practical significance.

To obtain satisfactory natural regeneration, certain biological requirements of the species must be met. These are: 1) abundant light; 2) a relatively constant water level; and 3) a satisfactory source of seed.

References

Anonymous. 1950. News of the world, Silviculture, U. S. A. Unasylva **4**: 183.

Averell, J. L., and P. C. McGrew. 1929. The reaction of swamp forests to drainage in northern Minnesota. Minn. State Dept. Drain. and Waters.

Baker, F. S. 1949. A revised tolerance table. Jour. Forestry **47**: 179-181.

———. 1950. Principles of silviculture. McGraw-Hill Book Co., New York.

Baldwin, Henry I. 1942. Forest tree seed. Chronica Botanica Co., Waltham, Mass.

Bates, Carlos G. 1923. Physiological requirements of Rocky Mountain trees. Jour. Agr. Res. **24**: 97-164.

———. 1925. The relative light requirements of some coniferous seedlings. Jour. Forestry **23**: 869-879.

Burns, G. P. 1923. Studies in tolerance of New England forest trees. IV. Minimum light requirement referred to a definite standard. Univ. Vt. Agr. Exp. Sta. Bull. **235**.

Burt, William H. 1946. The mammals of Michigan. Univ. Mich. Press, Ann Arbor, Mich.

Chapman, H. H. 1926. Factors determining natural reproduction of long-leaf pine on cutover lands in LaSalle Parish, La. Yale Univ. Sch. For. Bull. **16**.

Cheyney, E. G. 1942. American silvics and silviculture. Univ. Minn. Press, Minneapolis.

Conrad, J. P., and F. J. Veihmeyer. 1929. Root development and soil moisture. Hilgardia **4**: 113-134.

Conway, Verona M. 1949. The bogs of central Minnesota. Ecological Monog. **19**: 173-206.

Cooley, Grace E. 1903. Silvicultural features of *Larix americana.* For. Quart. **2**: 148-160.

Cooper, W. S. 1911. Reproduction by layering among conifers. Bot. Gaz. **52**: 369-379.

———. 1913. The climax forest of Isle Royale, Lake Superior and its development. Part III. Bot. Gaz. **55**: 189-235.

Cox, W. T. 1911. Reforestation on the National Forests. U. S. Dept. Agr. For. Serv. Bull. **98**.

Craib, Ian J. 1929. Some aspects of soil moisture in the forest. Yale Univ. Sch. For. Bull. **25**.

Davis, Wilmer E. 1939. An explanation of the advantage of alternating temperatures over constant tem-

peratures in the germination of certain seeds. Amer. Jour. Bot. **26**: 17s-18s.

Davis, Wm. C., George Y. Young, Dennis H. Latham, and Carl P. Hartley. 1938. Diseases of conifers in forest nurseries. U. S. Dept. Agr. Mimeo.

DeBoer, Stanley G. 1947. The deer damage to forest reproduction survey. Wis. Cons. Bull. **12**: No. 10.

Demaree, D. 1933. Submerging experiments with *Taxodium*. Ecology **13**: 258-262.

Doyle, Joseph. 1918. Observations on the morphology of *Larix leptolepis*. Sci. Proc. Roy. Soc. Dublin **15**: 310-330.

Duncan, Donald P. 1952a. Autecological studies of important forest trees. Ecology **33**: 285-286.

———. 1952b. Reproduction cutting in tamarack. Minn. Forestry Note **7**, Sch. For., Univ. Minn.

Eyre, F. H., and R. K. LeBarron. 1944. Management of jack pine stands in the Lake States. U. S. Dept. Agr. Tech. Bull. **863**.

Fowells, H. A. 1944. Site preparation as an aid to sugar pine regeneration. Calif. For. and Range Exp. Sta. Res. Note **41**.

Gates, Frank C. 1942. The bogs of northern Lower Michigan. Ecological Monog. **12**: 214-254.

Graves, Henry S. 1908. The study of natural reproduction of forests. For. Quart. **6**: 115-137.

Gunderson, Harvey L. 1950. A study of some small mammal populations. Occasional Paper **4**, Minn. Mus. Nat. Hist., Univ. Minn. Press, Minneapolis.

Haack, O. H. A. 1906. Über die Keimung und Bewertung des Kiefernsamens nach Keimproben. Zeit. f. Forst. und Jagdw. **38**: 441-475.

Haig, I. T. 1936. Factors controlling initial establishment of western white pine and associated species. Yale Univ. Sch. For. Bull. **41**.

Haig, I. T., K. P. Davis, and R. H. Weidman. 1941. Natural regeneration in the western white pine type. U. S. Dept. Agr. Tech. Bull. **767**.

Harrington, G. T. 1921. Optimum temperatures for flower seed germination. Bot. Gaz. **72**: 337-358.

Hartley, Carl. 1921. Damping-off in forest nurseries. U. S. Dept. Agr. Bull. **934**.

Hartley, Carl, T. C. Merrill, and Arthur S. Rhoades. 1918. Seedling diseases of conifers. Jour. Agr. Res. **15**: 521-558.

Hodson, A. C. 1951. How go the seasons? Minnesota Farm and Home Science **8**: 2; 15.

Hoene, John V. 1951. Wringing out a spruce bog. Amer. Forests **57**: 3; 20-21.

Hofmann, J. V. 1918. The importance of seed characteristics in the natural reproduction of coniferous forests. Univ. Minn. Studies in the Biol. Sci. **2**.

Isaac, Leo A. 1938. Factors affecting establishment of Douglas fir seedlings. U. S. Dept. Agr. Circ. **486**.

———. 1943. Reproductive habits of Douglas fir. Charles Lathrop Pack For. Found., Washington, D. C.

Jemison, G.M., and C. F. Korstian. 1944. Loblolly pine seed production and dispersal. Jour. Forestry **42**: 734-741.

Lawrence, D. B. 1951. Unpublished data.

LeBarron, R. K. 1944. Influence of controllable environmental conditions on regeneration of jack pine and black spruce. Jour. Agr. Res. **68**: 97-119.

———. 1948. Silvicultural management of black spruce in Minnesota. U. S. Dept. Agr. Circ. **791**.

LeBarron, R. K., and John R. Neetzel. 1942. Drainage of forested swamps. Ecology **23**: 457-465.

Livingston, B. E., and R. Koketsu. 1920. The water supplying power of the soil as related to the wilting of plants. Soil Sci. **9**: 469-485.

Lowdermilk, W. C. 1925. Factors affecting reproduction of Engelmann spruce. Jour. Agr. Res. **30**: 995-1009.

Marshall, W. H. 1951. Unpublished data.

Mattoon, Wilbur R. 1916. Water requirement and growth of young cypress. Proc. Soc. Amer. Foresters **11**: 192-197.

Mayr, Heinrich. 1925. Waldbau auf naturgesetzlicher Grundlage. Berlin.

Moore, A. W. 1942. Shrews as a check on Douglas fir regeneration. Jour. Mammalogy **23**: 37-41.

Morinaga, T. 1926. Germination of seeds under water. Amer. Jour. Bot. **13**: 126-140.

Munns, E. N. 1938. The distribution of important forest trees in the United States. U. S. Dept. Agr. Misc. Pub. **287**.

Nelson, Lowell O. 1950. Factors influencing seed production in forest trees. Manuscript, Sch. Forestry, Univ. Minn.

Nelson, M. L. 1940. Light influences germination of southern pine seed. South. For. Notes **31**, So. For. Exp. Sta.

Oosting, Henry J. 1948. The study of plant communities. W. H. Freeman Co., San Francisco, Calif.

Rathbun-Gravatt, Annie. 1931. Germination loss of coniferous seeds due to parasites. Jour. Agr. Res. **42**: 71-92.

Roe, E. I. 1949. Sphagnum moss retards black spruce regeneration. Lake States For. Exp. Sta. Tech. Note **321**.

Rudolf, Paul O. 1950. Cold soaking—a shortcut substitute for stratification? Jour. Forestry **48**: 31-32.

Schantz-Hansen, T. 1931. Preliminary observations on the use of clear cut strips in handling black spruce. Jour. Forestry **29**: 1168-1172.

Schumacher, W. 1864. Die Physik des Bodens. Berlin. (Original not seen.)

Shirley, Hardy L. 1934. Observations on drought injury in Minnesota forests. Ecology **15**: 32-48.

———. 1935. Light as an ecological factor and its measurement. Bot. Rev. **1**: 355-381.

———. 1941. Restoring conifers to aspen lands in the Lake States. U. S. Dept. Agr. Tech. Bull. **763**.

———. 1943. Is tolerance the capacity to endure shade? Jour. Forestry **41**: 339-345.

Society of American Foresters (Committee on Forest Terminology). 1950. Forestry terminology. Soc. Amer. Foresters, Washington, D. C.

Sparhawk, W. H. 1918. Effect of grazing upon western yellow pine reproduction in central Idaho. U. S. Dept. Agr. Bull. **738**.

Tripp, Howard A. 1951. Correspondence with D. P. Duncan under date July 12, 1951.

United States Forest Service. 1948. Woody plant seed manual. U. S. Govt. Print. Off., Washington, D. C.

Wherry, Edgar T. 1922. Soil acidity preferences of some eastern conifers. Jour. Forestry **20**: 488-496.

Wiesner, J. 1907. Der Lichtgenuss der Pflanzen. Leipzig.

INHIBITORY EFFECTS OF PHYTOPLANKTON UPON THE FEEDING OF *DAPHNIA MAGNA* WITH REFERENCE TO GROWTH, REPRODUCTION, AND SURVIVAL[1, 2]

JOHN H. RYTHER[3]
Biological Laboratories, Harvard University, Cambridge, Massachusetts

INTRODUCTION

It has been frequently observed, with respect to both the seasonal and geographical distribution of marine plankton populations, that the zooplankton is often scarce in waters rich with phytoplankton, and, conversely, that the animals may be most abundant in areas containing relatively few of the plant cells. This situation formerly appeared to be contradictory to the popular concept that the animals are largely dependent upon the phytoplankton for their food. In recent years, however, several explanations for this distributional pattern have been suggested, the most frequently quoted being the theories of "grazing" and "animal exclusion."

The theory of "grazing" proposed by Harvey *et al.* (1935) holds that the extensive feeding of the herbivorous zooplankton rapidly decimates the crop of phytoplankton living in the same waters with the animals, making unlikely the coexistence of large populations of both plants and animals. This grazing effect of a large population of the herbivores may presumably remove completely the standing crop of phytoplankton, and high concentrations of the latter can therefore develop only in the paucity or absence of the animals.

Hardy's theory of "animal exclusion" (Hardy and Gunther 1935; Hardy 1936), on the other hand, contends that dense populations of phytoplankton produce conditions which are unfavorable for the zooplankton, and that the latter consequently avoid or are excluded from these high concentrations of the algae. The physiological basis of the exclusion was not investigated by Hardy, but was believed to result from an inimical effect, presumably chemical in nature, of the phytoplankton upon the animals. Because this has never been clearly demonstrated in the laboratory or otherwise, Hardy's theory has lost much of its original impetus.

There is growing evidence, however, that dense populations of phytoplankton, in both marine and freshwater habitats, may create conditions which are inimical or actually lethal to a great variety of aquatic organisms. The literature dealing with this subject is too extensive to review here. The list of organisms which have been found to be adversely affected by phytoplankton includes numerous species of fish (Hardy 1936; Otterström and Steemann Nielsen 1939), shellfish (Bückmann 1934; Nightingale 1936; Loosanoff and Engle 1947; Korringa 1950), and barnacles (Allison and Cole 1934, 1935). Certain freshwater phytoplankters have been found to produce substances which inhibit their own growth (Pratt and Fong, 1940 and other papers; Storey 1943) and the growth of other species of algae (Rice 1954; Lefèvre *et al.*, 1951 and earlier papers).

In view of this evidence, the possibility that large populations of phytoplankton may, under certain conditions, create an unfavorable environment for the zooplankton, with which they are intimately associated, seems more than likely.

Lucus (1938, 1947, 1949) has presented a series of reviews concerning non-predatory relations between groups of organisms mediated by the production of external metabolites or "ectocrines" by the one group which produce a stimulatory or inhibitory effect upon the other. While his examples have been drawn from many fields of biology, Lucas has proposed a relationship of this type between plankton organisms as an explanation of Hardy's "exclusion" theory. In this connection, he states (Lucas 1947) "Here may be briefly considered the possible mediation of 'animal exclusion' in which it now seems reasonable to see the more or less passive avoidance of certain plant products (those typical of peak numbers) which in some instances may prove fatal if they cannot be avoided. . . . The widespread occurrence of antibiotics elsewhere makes highly probable the existence of such processes in the sea."

In considering the relations between phytoplankton and zooplankton populations, the freshwater environment has been largely neglected. Such studies as have been made have, in most cases, failed to demonstrate any correlation between the two groups, *e.g.* Pennak (1947). However, since

[1] Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University, Cambridge, Massachusetts.

[2] Contribution No. 730 from the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

[3] Present address: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

the numerically important species of phytoplankton and the herbivorous zooplankton belong to the same taxonomic groups and presumably occupy the same ecological niches in freshwater as in the sea, then it must be assumed, in the absence of evidence to the contrary, that the same relations exist between the plants and animals in both cases.

The experiments which will be described below concern the relations between the freshwater cladoceran, *Daphnia magna* and three species of planktonic algae in which there is presented evidence of a mechanism which provides a physiological basis for the concept of "animal exclusion."

The author expresses his sincere appreciation to Dr. G. L. Clarke for his helpful suggestions and critical analysis of this work. The investigation was carried out under the sponsorship of a U. S. Atomic Energy Commission predoctoral fellowship.

Materials and Methods

Daphnia culture

Daphnia magna used in the experiments to be described below was obtained from stocks maintained at the Biological Laboratories of Harvard University. The animals were cultured in cement water tables measuring 66 x 24 inches in area which were kept filled to a depth of approximately 2 inches with constantly dripping tap water. The *Daphnia* lived in association with a population of snails, *Lymnaea palustris,* which was maintained by feeding regularly with lettuce. The *Daphnia* fed upon the fecal matter from the snails and its associated bacterial flora. This culture method proved to be extremely successful. Parthenogenetic reproduction occurred throughout the one-year period during which the experiments were in progress, eggs or young were always plentiful in mature animals, and no males or females with ephippia were ever observed.

Phytoplankton culture

Three species of algae were used for feeding *Daphnia* in the experimental work, the *Chlorophyta, Chlorella vulgaris* and *Scenedesmus quadricauda,* and the diatom, *Navicula pelliculosa.* The *Chlorella* was obtained in pure culture from Dr. W. T. Edmondson, and bacteria-free cultures were used for all experiments. *Scenedesmus,* which was isolated from a pond in Belmont, Mass., and *Navicula,* which was provided by Dr. Ruth Patrick, were maintained and used in unialgal but not pure cultures.

Algae were cultured in 10-liter batches in Pyrex jugs illuminated by water-cooled, immersed neon U-tubes and aerated with 5% CO_2, as described by Scott (1943). Smaller, 500-ml. flask cultures illuminated by a bank of daylight fluorescent lamps were also used. The same nutrient medium was used for growing all three species of algae and consisted of the following salts and concentrations:

Standard culture medium (Rice 1949)	
$Ca(NO_3)_2 \cdot 4H_2O$	0.004%
$MgSO_4 \cdot 7H_2O$	0.002
KCl	0.004
$Na_2SiO_3 \cdot 9H_2O$	0.0025
$FeCl_3$	0.0001
KH_2PO_4	0.002
A-Z solution	0.100

"A-Z" solution is a mixture of trace elements described as "Solution A" by Hoagland and Snyder (1933). The growth of all algal cultures was determined from cell counts made at intervals of 2-3 days with a Levy hemacytometer.

Feeding experiments

Feeding experiments were conducted in a constant-temperature room maintained at 18-20° C. and were illuminated by an overhead fluorescent lamp providing 64 foot candles of light to the experimental vessel.

Daphnia were removed from their culture tank, washed in filtered pond water, and conditioned to the experimental temperature and illumination for 24 hours prior to each experiment.

Algae to be used in the experiments were centrifuged from their culture media and resuspended in filtered pond water to insure that a minimum of any substance, either metabolites of the algae or their mineral nutrients, would be carried over into the feeding experiment. This suspension of the algae was further diluted with filtered pond water to produce the desired concentration of cells as determined from hemacytometer counts.

Twenty-five *Daphnia* were then placed in a 100-ml. aliquot of the diluted algal suspension and allowed to feed for one hour. At the beginning and end of the one-hour period samples were withdrawn from the experimental vessel and the concentration of cells in each sample was determined from hemacytometer counts.

The filtering rate of the *Daphnia,* described for the purposes of these experiments as the number of ml. of water from which all cells have been removed per *Daphnia* per hour, was calculated by the same method as used by Gauld (1951) for marine copepods. Assuming the animals to be constant feeders, the concentration of cells in the water in which they are feeding will decrease exponentially according to the equation:

$$C_t = C_0 e^{-kt}$$

where C_t is the concentration at time t and C_0 is the initial concentration.

Filtering rate (F) may then be calculated from the equation:

$$F = vk$$

where v is the volume of water per *Daphnia*.

C_0 and C_t were determined by taking the mean of a series of 36-48 cell counts of 0.4 mm³ hemacytometer fields of samples taken at the beginning and end of the experiment. Concentrations calculated in this manner gave a coefficient of variability ranging from 1% to 3%. Filtering rates determined in a series of identical feeding experiments gave a coefficient of variability of 10-20%.

Feeding experiments were conducted with all three species of algae using concentrations ranging from 0.1 to 0.6 million cells per milliliter.

Experiments were limited to a one-hour period to avoid the introduction of errors caused by the settling of cells during the feeding period. Controls containing algal suspensions with no *Daphnia* showed agreement between initial and final counts within the range of counting error for one-hour experiments, but showed a decrease after four hours often greater than the number of cells removed by the animals. Agitation or other methods of keeping the cells in suspension interferred with the normal activity of the animals and often stopped their feeding entirely.

Experiments

A. The relation between the size of Daphnia and its feeding rate

Using the methods described above, four groups each of 25 *Daphnia* measuring respectively 1.5, 2.0, 2.5, and 3.0 mm. in length were fed *Chlorella*. In each experiment the same initial concentration of 0.20 million *Chlorella* per ml. was employed. Following each experiment, the *Daphnia* were dried for 24 hours at 60° C. and weighed.

On the basis of three experiments with each of the four size groups the mean number of *Chlorella* consumed per hour per mg. dry weight of *Daphnia* was calculated for animals of each size.

Food consumption per mg. dry weight plotted against the size of the *Daphnia*, also expressed in mg. dry weight, clearly indicates a straight line relationship, with *Chlorella* consumption an inverse function of size. (Fig. 1). From the straight line drawn through the four points by the method of least squares a curve was constructed showing the relation between size and food consumption per *Daphnia* (Fig. 1). This curve shows that maximum food consumption occurs in animals with a dry weight of 0.11-0.12 mg. (2.7-2.8 mm. in length).

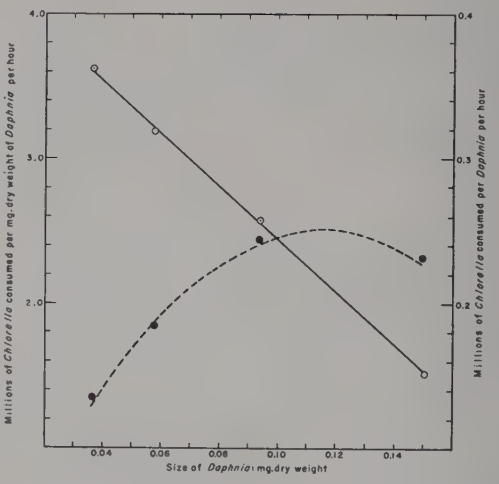

Fig. 1. Relation between the size of *Daphnia* and its feeding rate. *Chlorella* consumed per mg. dry weight of *Daphnia*-◎- ; *Chorella* consumed per *Daphnia* --●--.

It is also obvious that feeding rate in different-sized animals is much less variable when expressed per *Daphnia* rather than per unit of weight. Consequently, filtering rates in the following experiments have been calculated on that basis. Furthermore, experimental animals have been limited to a size range of 0.095-0.135 mg. dry weight (2.5-2.9 mm. length), within which variations in feeding rate due to size could be neglected.

B. Filtering rates of Daphnia feeding upon growing Chlorella

In a series of 86 one-hour feeding experiments, *Daphnia* were fed *Chlorella* from cultures which were in their log phase of growth. *Daphnia* used for this series were starved for 24 hours prior to the experiments and their intestinal tracts were completely empty except for a small plug of feces at the end of the gut. From five to ten experiments were made at each of 12 concentrations of *Chlorella* ranging from 0.05 to 0.60 million cells per ml. at intervals of approximately 0.05 million cells per ml. Following each experiment the filtering rate and the average of the initial and final concentration of *Chlorella* were calculated. Figure 2 shows the relationship between filtering rate and *Chlorella* concentration, each point representing the mean filtering rate and the mean average concentration of *Chlorella* of the five to ten experiments in which the *Daphnia* were fed approximately the same concentration of cells. It is at once obvious that there is an inverse relationship between filtering rate and the concentration of food, with the former decreasing as the latter in-

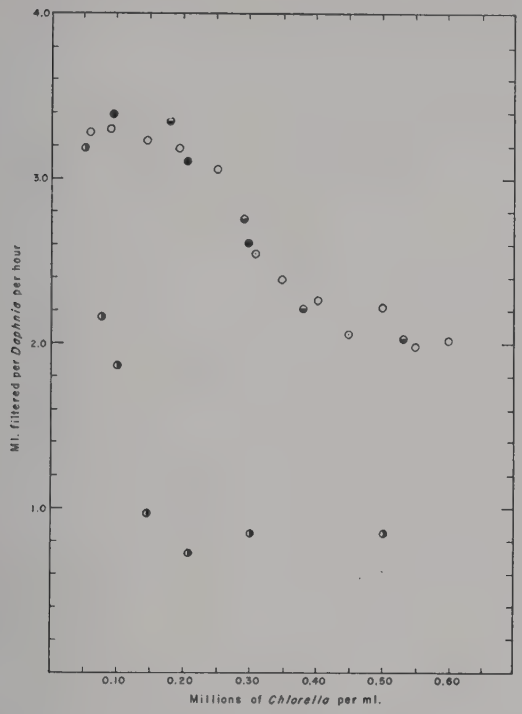

FIG. 2. Filtering rates of *Daphnia* feeding upon growing *Chlorella*. Starved *Daphnia* ◎ ; *Daphnia* fed detritus and bacteria prior to experiments ● ; starved *Daphnia* in media conditioned with growing *Chlorella* prior to experiments ◒ ; *Daphnia* fed growing *Chlorella* for 12 hours prior to experiments ◑ .

creases. This relationship is apparent within the entire range of the *Chlorella* concentrations which were used, but is most obvious at the intermediate concentrations of 0.2-0.5 million cells per ml.

An obvious explanation for this behavior is that the starved *Daphnia* decreased their feeding effort as they filled up with the algae. The higher the concentration of cells in which they are placed, the more rapidly they should be able to do this, and the lower would be the resulting hourly filtering rate.

To test this theory, three feeding experiments were conducted at *Chlorella* concentrations of approximately 0.1, 0.2, and 0.3 million cells per ml., using *Daphnia* which were conditioned to the experimental conditions for 24 hours in water taken from their culture tanks rather than in filtered pond water. These animals, in contrast to those used in the preceding experiments, had their intestinal tracts completely full of a black mass of food matter at the beginning of the experiments. These experiments were repeated twice using the same three concentrations of *Chlorella* each time, and the means were taken as before. The results indicate that the well-fed *Daphnia* filter at essentially the same rate as the starved animals feeding upon the same concentrations of cells (Fig. 2).

It may be concluded, therefore, that the amount of food, in itself, in the intestinal tracts of the *Daphnia* was not the factor responsible for the decrease in the filtering rates of animals feeding in progressively higher concentrations of *Chlorella*. Apparently, then, this effect resulted from some characteristic of the algae themselves.

Pratt and Fong (1940) demonstrated that *Chlorella vulgaris* produces and releases into its external medium a substance which inhibits its own growth. Later studies (Pratt *et al.* 1944) disclosed that this substance, named chlorellin by its discoverers, is antibiotic against gram-positive and gram-negative bacteria.

In view of this work, it appeared likely that the observed depression of the filtering rate of *Daphnia* might be mediated by the antibiotic, chlorellin, acting upon the animals either in solution in the water in which they feed, or within the *Daphnia* through its release from ingested cells.

The following series of experiments was designed to investigate whether chlorellin in solution in the water in which *Daphnia* are feeding could account for the depression of the filtering rate as observed in the preceding experiments. A culture of *Chlorella* in its log phase of growth was centrifuged and the cells resuspended in filtered pond water producing a concentration of 0.478 million cells per ml. After a period of 48 hours, during which the suspension was illuminated and agitated, the cells were removed by filtration. To this "conditioned" water, *Chlorella* and *Daphnia* were then added in the same manner as described above for the preceding experiments, and the filtering rate of the animals was measured as before. Initial concentrations of *Chlorella* were approximately 0.2, 0.3, 0.4, and 0.5 million cells per ml. and four to five experiments were performed at each of these concentrations. The mean filtering rate of these animals plotted against *Chlorella* concentration shows no significant difference from that of animals feeding upon the same concentrations of the algae in "unconditioned" water (Fig. 2).

In the series of experiments in which "unconditioned" water was used, there was a period of just one hour, the duration of the experiment, during which substances could have diffused from the algae into the *Daphnia's* surrounding medium. Since a relatively high concentration of *Chlorella* suspended in the water for an additional 48 hours

did not further depress the filtering rate of the animals, the inhibition of feeding observed in these experiments apparently did not result from the accumulation of chlorellin or similar substances from the algae in the water.

A further possibility exists, however, that the inhibitory products of the algae produce their effect upon being released from ingested cells and assimilated by the *Daphnia*. The results of the experiments which were described above can be explained quite satisfactorily on the basis of such a theory.

If it may be assumed that the starved *Daphnia* were feeding at a constant "uninhibited" rate at the onset of the experiments, then this rate will decrease during the one-hour period as the animals ingest *Chlorella* cells and assimilate their inhibitory products. Thus the calculated filtering rate represents an average for the one-hour feeding period. The higher the concentration of *Chlorella* in the water at the beginning of the experiment, the greater will be the rates of ingestion of cells and assimilation of their inhibitory products, and the lower will be the average filtering rate.

It was noted above that at *Chlorella* concentrations between 0.05 and 0.25 million cells per ml. the depression of the filtering rate with increasing cell concentrations was very slight. Microscopic examination of *Daphnia* after feeding for one hour upon *Chlorella* within this range of concentrations disclosed the presence of relatively few cells in their intestinal tract.

In the process of feeding, *Daphnia* collects the filtered food particles in a ventral groove at the base of its thoracic appendages, whence the food is passed forward to the mouth and into the intestinal tract. Therefore, an appreciable number of cells must be filtered before any of them reach the absorptive part of the intestine, and in *Daphnia* feeding upon low concentrations of food organisms this may require a considerable period of time.

It would seem likely, therefore, that the *Daphnia* which were feeding upon *Chlorella* at concentrations below 0.25 million per ml. did not assimilate enough of the inhibitory substance to decrease their filtering rate in the course of the one-hour experiment.

Daphnia feeding upon *Chlorella* at concentrations exceeding 0.5 million cells per ml., on the other hand, were observed to fill completely their intestinal tracts with green cells within the course of the experiments, and these animals defecated green masses of apparently undigested algae for the remainder of the feeding period. With such high concentrations of the algae in the external medium of *Daphnia*, the cells appear to pass through the intestine so rapidly that efficiency of digestion is greatly reduced. It follows that the efficiency of assimilation of the inhibitory products of the algae is similarly reduced, and that the higher the concentration of the algae in the water, the lower that efficiency will be. This is believed to be the explanation of the fact that, with increasing concentrations of *Chlorella* above 0.5 million cells per ml., further decrease in the filtering rate of *Daphnia* is very small.

Daphnia which have been feeding continuously, or for long periods of time, upon *Chlorella* at any given concentration would be expected to feed at some constant rate. This rate should be considerably lower than that calculated in the preceding experiments for *Daphnia* feeding upon the same concentration of *Chlorella* for just one hour, where the filtering rate, as determined, represented a rate which was decreasing throughout most or all of the experimental period. An attempt has been made in the following series of experiments to measure the filtering rates of *Daphnia* which had been feeding upon various concentrations of *Chlorella* for periods of 12 hours prior to the experiments.

Groups of 25 *Daphnia* were placed in two-liter suspensions of log-phase *Chlorella* in filtered pond water at seven different concentrations of cells ranging from 0.05 to 0.50 million cells per ml. Every three hours the animals were transferred to a fresh suspension of the algae so that they were unable to lower the concentration in any case by more than 10%. The animals were allowed to feed in these suspensions of algae for a period of 12 hours. Following this, the *Daphnia* were transferred to small experimental vessels containing 100-ml. suspensions of the same concentrations of *Chlorella* upon which the animals had been previously feeding, and their filtering rates were determined as before for an additional one-hour period.

The mean filtering rate for three experiments conducted at each concentration of the algae was, in every case, considerably lower than that of starved *Daphnia* which had fed upon the same concentrations of *Chlorella* for just one hour (Fig. 2).

Above concentrations of 0.15 million cells per ml. the filtering rates appear to be rather constant, ranging from 0.72 to 0.96 ml. per *Daphnia* per hour. It was also observed that after animals had fed upon *Chlorella* at or above this concentration for 12 hours, their intestinal tracts were completely full of green cells. As mentioned above this situation apparently results in a minimum, constant filtering rate.

The *Daphnia* feeding upon 0.05 million *Chlorella* per ml. for 13 hours (12 hours' conditioning plus the experimental period) filtered at essentially the same rate as the starved animals which fed upon the same concentration of the algae for just one hour. It was postulated above that this represents the maximum, uninhibited filtering rate of the animals. It appears, therefore, that they were unable in 13 hours to consume enough algae at that concentration to be affected by their inhibitory products. At *Chlorella* concentrations between 0.05 and 0.15 million cells per ml. intermediate filtering rates were observed.

Whether or not an equilibrium had actually been reached by 12 hours was not determined. Presumably, however, there is a concentration of cells below which *Daphnia* are unable to keep their intestinal tracts filled with the algae no matter how long they feed, and another concentration below which continually feeding *Daphnia* can never consume sufficient *Chlorella* to be affected by the inhibitory products of the algae. Within the range determined by these two concentrations, the filtering rates of *Daphnia* feeding upon *Chlorella* under natural conditions would appear to be determined by the concentration of the algae in the water.

C. The filtering rates of Daphnia feeding upon senescent Chlorella

Studies by Pratt, Oneto, and Pratt (1945) revealed that the production of the antibiotic, chlorellin, is related to the physiological condition of the *Chlorella*. In cultures where the cells have a high division rate and the population is increasing exponentially, little or no chlorellin is released into the water, while senescent, static populations of the algae were found to produce the substance at maximum rates.

Care was taken in the experiments described in Section *B* to use only *Chlorella* from cultures which were growing exponentially. If the depression of the filtering rate of *Daphnia* feeding upon increasing concentrations of this actively growing *Chlorella* was due to the assimilation of chlorellin by the animals, then this inhibition should be more pronounced in the case of *Daphnia* feeding upon more slowly dividing algae. It may be noted in this connection that feeding rates reported in Section *A* are considerably lower than those observed in *Daphnia* feeding upon the same concentration of log phase *Chlorella* (cf. Figs. 1 and 2). Unfortunately data are not available concerning the growth phase of the *Chlorella* used in the former series of experiments. However, the relatively low filtering rate of the animals is suggestive of an increased inhibition possibly resulting from a more slowly dividing population of algae with a higher chlorellin concentration. To investigate this matter further, a series of experiments was performed similar to those reported in Section *B* with the exception that senescent, non-dividing *Chlorella* were used.

In experiments in which starved *Daphnia* were fed increasing concentrations of senescent *Chlorella* suspended in filtered pond water, the filtering rate was much lower at any concentration than that of animals feeding upon the corresponding concentration of log-phase *Chlorella* (Fig. 3).

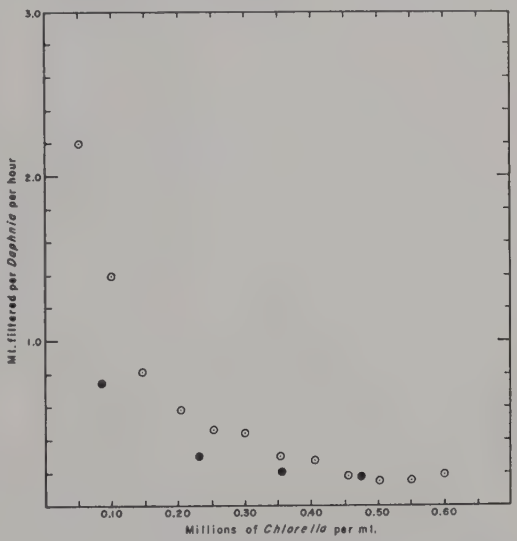

FIG. 3. Filtering rates of *Daphnia* feeding upon senescent *Chlorella*. Starved *Daphnia* ◎; Starved *Daphnia* in media conditioned with senescent *Chlorella* prior to experiments ●.

The same decrease in filtering rate with increasing cell concentrations of the senescent *Chlorella* occurs as in the case of *Daphnia* feeding upon the actively growing algae. However, it is noteworthy in this case that the *Daphnia* removed from the water approximately the same number of cells in one hour regardless of the concentration, in contrast to the animals feeding upon growing *Chlorella* where, despite a decreasing filtering rate, the *Daphnia* consumed increasingly larger amounts of *Chlorella* as the concentration of cells in the water increased (Table I). This trend is most obvious at *Chlorella* concentrations below 0.45 million cells per ml. and is somewhat obscured at higher concentrations because of the fact that error in estimating cell concentrations increases with the concentration.

TABLE I. *The numbers of log-phase and senescent* Chlorella *filtered by* Daphnia *feeding upon various concentrations of the algae.*

Approximate mean conc. of *Chlorella*. (cells/ml. x 10^6)	Log-phase *Chlorella* filtered. (cells x 10^6/hr./*Daphnia*)	Senescent *Chlorella* filtered. (cells x 10^6/hr./*Daphnia*)
0.05	0.20	0.11
0.10	0.30	0.14
0.15	0.48	0.12
0.20	0.62	0.12
0.25	0.77	0.12
0.30	0.78	0.13
0.35	0.83	0.11
0.40	0.91	0.11
0.45	0.92	0.08
0.50	1.10	0.07
0.55	1.03	0.08
0.60	1.20	0.11

The fact that *Daphnia* feeding upon the senescent *Chlorella* appear to consume approximately the same amounts of the algae regardless of its concentration in the water suggests that the animals cease feeding entirely after the ingestion of a certain number of these cells. This recalls the earlier comment that a given number of cells must be filtered from the water before any of them reach the intestinal tract.

To determine whether chlorellin released into the water from the senescent algae could affect the filtering rate of *Daphnia,* filtered pond water was conditioned with a suspension of 0.5 million nondividing *Chlorella* for 48 hours. The algae were then removed by filtration and senescent *Chlorella* and *Daphnia* were added to the conditioned water and the filtering rates of the animals measured as before. Results of four to six experiments at each of four concentrations of the algae show that a further inhibition of the filtering rate was produced by the conditioned water in the experiments in which *Daphnia* were fed senescent *Chlorella* at concentrations below 0.3 million cells per ml. (Fig. 3). Above this concentration there was no appreciable difference between the experiments in which conditioned and unconditioned water were used. Presumably at the higher concentrations of the algae sufficient cells are consumed within the first few minutes of the experiment to cause the animals to cease feeding, and the effect of the chlorellin in solution is masked.

In a third series of experiments with senescent *Chlorella, Daphnia* were placed in various concentrations of the algae for 12 hours prior to the measurement of their filtering rates for an additional hour, in the same manner as in the similar series in which growing *Chlorella* was used. After 12 hours of exposure to the senescent *Chlorella,* none of the *Daphnia* showed any signs of having fed during the ensuing one hour experiment. Even at concentrations as low as 0.05 million cells per ml. there was no significant difference between cell counts at the beginning and end of the feeding period. Examination of the *Daphnia* showed no trace of the algae in their intestinal tracts.

D. Feeding experiments with Navicula and Scenedesmus

Feeding experiments similar to those described above were performed with starved *Daphnia* feeding for periods of one hour upon the diatom *Navicula pelliculosa* and the chlorophyte *Scenedesmus quadricauda.* The animals were fed both rapidly growing and senescent cells of both species at various concentrations. *Scenedesmus* is a colonial form which occurs as single cells or, more commonly, as two- or four-celled coenobia. The filtering rates of *Daphnia* feeding upon this species were calculated on the basis of particles rather than single cells consumed.

The results of experiments with these two species of algae were similar in all respects to those in which the animals were fed *Chlorella* with the exception that the magnitude of the variations of the filtering rate was not so great under the different conditions which were studied. (Figs. 4, 5.) If the observed depression of the filtering rate of *Daphnia* feeding upon *Chlorella* resulted from the inhibitory product of the algae, chlorellin, then it must follow that both *Navicula* and *Scenedesmus* produce substances of a similar nature

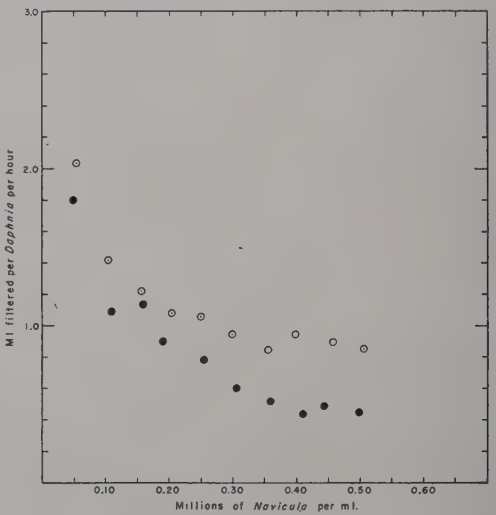

FIG. 4. Filtering rates of starved *Daphnia* feeding upon growing *Navicula* ◎ and senescent *Navicula* ● .

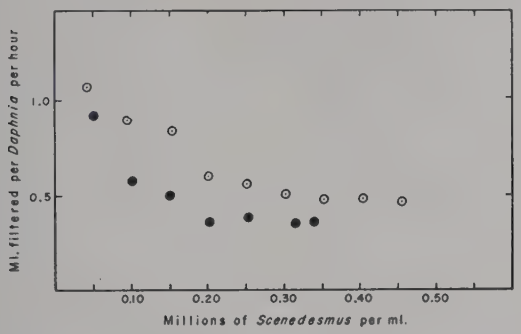

FIG. 5. Filtering rates of starved *Daphnia* feeding upon growing *Scenedesmus* ◎ and senescent *Scenedesmus* ●.

which also act as inhibitors upon the feeding process of the cladoceran.

At any given concentration of algae in the same physiological condition, *Daphnia* were observed to feed most rapidly upon *Chlorella* and at the lowest rate upon *Scenedesmus*. This appears to be related to the size of the algae. Average cell volumes of *Chlorella* and *Navicula* were 3.5 μ^3 and 9.2 μ^3 respectively, and the average volume of the *Scenedesmus* coenobia was 25.5 μ^3.

The possibility was considered that the animals filtered the larger species of algae less efficiently than the smaller *Chlorella* cells. However, in a series of six experiments in which *Daphnia* were fed mixed cultures containing equal numbers of *Scenedesmus* and *Chlorella*, the same number of each species was consumed in one hour (Table II).

TABLE II. *The rates of consumption of* Chlorella *and* Scenedesmus *by* Daphnia *feeding upon mixed cultures of the algae.*

Mean concentration of algae. (cells or colonies/ml. x 10^6)		Cells or colonies consumed/ *Daphnia*/hour x 10^6	
Chlorella	*Scenedesmus*	*Chlorella*	*Scenedesmus*
.175	.174	.22	.25
.179	.169	.24	.24
.178	.180	.24	.25
.181	.183	.26	.25
.170	.184	.24	.22
.159	.170	.27	.26

Since it has already been demonstrated that the amount of food consumed by the *Daphnia* does not, in itself, affect the filtering rate of the animals, it must be assumed that the different algae here considered produce different amounts of the inhibitory substances per cell, a likely possibility in view of their difference in size, or that these substances differ in their effect upon the *Daphnia*.

E. The effects of the age of Chlorella upon the growth, reproduction, and survival of Daphnia

In view of the marked difference between the rates at which *Daphnia* feed upon rapidly growing and senescent populations of *Chlorella*, the following experiment was designed to demonstrate the longer-term effects which the algae in these two conditions might have upon the growth, reproduction, and longevity of *Daphnia*.

Ten cultures were inoculated each with 25 *Daphnia* which were born the day the experiment began. These animals, all from the same clone, averaged 1.0 mm. in length at the start of the experiment. The cultures consisted of finger bowls containing 200 ml. of filtered pond water. Cultures 1-5 were fed *Chlorella* in its log phase of growth and cultures 6-10 were fed senescent *Chlorella*. All cultures were fed at the rate of 50 million cells per day for the first six days and 100 million cells per day thereafter. Every day prior to feeding, the water in each culture was replaced with fresh, filtered pond water, and any animals which had died or had been born during the previous 24 hours were removed. Every three days 10 animals were removed at random from each of the two groups of cultures and measured.

The results of the experiment are summarized in Table III showing the average number of young and the average number of deaths per culture per day and the average size of the 10 animals measured every three days for the two groups of cultures.

The animals which were fed log-phase *Chlorella* grew rapidly throughout the 13 day experiment and by the 12th day had reached a high rate of reproduction. No animals died in this group.

TABLE III. *The growth, reproduction, and longevity of* Daphnia *which were fed actively growing and senescent* Chlorella.

Days	*Daphnia* fed growing *Chlorella*			*Daphnia* fed senescent *Chlorella*		
	Av. size mm.	Young per culture	Deaths per culture	Av. size mm.	Young per culture	Deaths per culture
1.....	1.0	0	0	1.0	0	0
2.....	...	0	0	...	0	0
3.....	...	0	0	...	0	0
4.....	1.6	0	0	1.3	0	0
5.....	...	0	0	...	0	0
6.....	...	0	0	...	0	0
7.....	2.2	0.4	0	1.4	0	0
8.....	...	2.0	0	...	0	0
9.....	...	8.0	0	...	0	0
10.....	2.6	17.6	0	1.5	0	0.6
11.....	...	16.0	0	...	0	5.6
12.....	...	45.6	0	...	0	9.2
13.....	2.9	43.4	0	—*	0	9.6

*All animals dead

Those which were fed senescent *Chlorella* grew very slowly with no evidence of ecdysis during the experiment. No young were produced nor were eggs observed in any individual in this group. These animals were completely unpigmented in contrast to the reddish-brown color of the *Daphnia* which were fed growing *Chlorella,* and they were relatively inactive, spending most of their time resting on the bottom of the finger bowls. They began to die on the 10th day and were all dead by the 13th day, thereby ending the experiment.

Discussion

The experiments which have been described in this report represent, to the author's knowledge, the first extensive study of the feeding rate of a freshwater, filter-feeding zooplankton organism. The only work with which it may be compared, therefore, is that of investigators who have studied the feeding habits of marine zooplankton.

Clarke and Fuller (1936), in the first preliminary work on this subject, found that the filtering rate of *Calanus finmarchicus* feeding upon carmine particles averaged, in six experiments, 5.6 ml. of water filtered per animal per 24 hours. In an extension of that work, Fuller (1937) fed *Calanus* upon the diatom, *Nitzschia closterium,* using a range of concentrations from 0.002 to 0.41 million cells per ml. From a series of 12 feeding experiments within that range, he observed an average filtering rate of 1.08 ml. per *Calanus* per 24 hours.

Lucas (1936), also using *Nitzschia* as a food organism, conducted feeding experiments with the copepod, *Eurytemora hirundoides,* and the mysid, *Neomysis vulgaris.* His experiments, which involved a wide range of concentrations of the diatom, showed mean filtering rates of 2.9 ml. per copepod and 0.011 ml. per mysid per 24 hours, but the results of both series showed a coefficient of variability of over 75%.

Fuller and Clarke calculated, from the daily food requirements of *Calanus* as given by Marshall, Nicholls, and Orr (1935), that stage V *Calanus* would require a minimum filtering rate of 72 ml. per 24 hours in order to subsist upon the various components of the phytoplankton and nannoplankton occurring in Vineyard Sound at a time when the copepod was abundant there. This figure is at considerable variance with the observed filtering rates of *Calanus* discussed above.

Harvey (1937), however, observed that while *Calanus* fed upon *Nitzschia* at a rate of only 4.56 ml. per animal per 24 hours, the copepod fed upon the larger diatoms, *Lauderia borialis* and *Ditylum brightwelli,* at rates of 48-96 ml. and 168-240 ml. per animal per 24 hours respectively.

Fuller interpreted this to mean that the smaller *Nitzschia* passed through the filtering mechanism of the copepod, and, in consequence, the filtering process was relatively inefficient with particles of that size. This seems rather doubtful in view of the success of Raymond and Gross (1942) in culturing *Calanus* upon flagellates 1-2 μ in diameter, organisms an order of magnitude smaller than *Nitzschia.*

Furthermore, Gauld (1951), who has probably made the most extensive study of the feeding of marine zooplankton, observed that the filtering rate of stage V *Calanus* feeding upon a marine *Chlamydomonas* averaged 64 ml. at 12.5° C. and 95 ml. at 17° C. per animal per 24 hours. These figures show a reasonable agreement with those of Harvey for *Calanus* feeding upon the larger diatoms. However, Gauld points out that the *Chlamydomonas* used in his work was considerably smaller than the *Nitzschia closterium* forma *minutissima* used by both Fuller and Harvey. Hence differences in the size of the food organisms can hardly account for the observed variability in the filtering rate of the copepod.

In none of the work which has been described above was there observed any tendency for the animals to decrease their filtering rates in increasing concentrations of the food organisms. As a result, the opinion now appears to be widely accepted that these grazers filter at a constant rate, at a given temperature, which is unaffected by the concentration or other characteristics of the food in the water (Lucas 1936; Fuller 1936; Fleming 1939; Harvey 1942; Riley 1946, 1947.)

However, not only were the experimental results reported by the individual workers in every case extremely variable, but filtering rates of the same animal feeding upon different species of food organisms, as reported by different authors, were in some cases not of the same order of magnitude. Since fundamentally the same methods were used in every case, these variations are hardly consistent with the concept of a fixed, constant, filtering rate.

The feeding experiments with *Daphnia* have demonstrated that, within a limited range, the concentration of algae in the water may have a pronounced effect upon the filtering rate of that animal. Of even greater importance, however, is the physiological condition, or population age, of the phytoplankton in its effect upon the feeding of the cladoceran. The latter appears to be a factor which has hitherto not been considered in this respect.

The combination of the two factors, concentration and age of the phytoplankton population, was found to produce a range in the filtering rate of *Daphnia* from a maximum of 81 ml. per animal per 24 hours to a value approaching or equalling zero. It is perhaps significant that this range closely approximates that observed by Fuller and Gauld for stage V *Calanus,* an animal similar in size to *Daphnia.*

In view of the similarity of the inhibitory effects, insofar as they were studied, of the three species of algae upon *Daphnia,* and the widespread occurrence of inhibitory or toxic effects of phytoplankton upon a great variety of other aquatic organisms, as reported elsewhere, it is not unreasonable to propose a relationship of this type between natural populations of phytoplankton and zooplankton filter feeders. Here may be reconsidered briefly the frequently reported inverse correlation between the abundance of phytoplankton and zooplankton which was discussed in the opening of this paper with a re-evaluation of Harvey's grazing theory and Hardy's concept of "animal exclusion."

The ideal food for *Daphnia* appears to consist of young, actively dividing populations of phytoplankton. In that state, the algae are fed upon by the animals with great rapidity. With high concentrations of the cells in the water, they are consumed at rates which are greatly in excess of the *Daphnia's* nutritional requirements, and a large fraction of the ingested algae pass through the animal's intestine unassimilated.

A similar situation was reported by Harvey *et al.* (1935) in the English Channel during 1935 and 1936. There, the spring diatom blooms for those years were observed to disappear suddenly, although nutrients and other conditions appeared to be favorable for the continued growth of the plants. The simultaneous increase in the numbers of large copepods, and the observation of quantities of the fecal pellets of the animals colored green with chlorophyll led these workers to the conclusion that the phytoplankton crop was depleted by the extensive grazing of the herbivores.

In *Daphnia* this situation may obtain only so long as the phytoplankton cells are actively dividing. If, in a natural situation, conditions become favorable for an eruptive growth of phytoplankton, the latter may grow at a higher rate than they can be removed by grazing. The algal population will then no longer be limited by the animals, but will increase until its supply of nutrients becomes exhausted. As the population peak is approached, inhibitory substances accumulate in the algal cells, and they presumably no longer represent a suitable food for the grazers.

The experimental *Daphnia,* confined to the same water mass as the senescent phytoplankton, ceased feeding and eventually died. In an open body of water, it is more likely that actively swimming animals would be able to avoid these concentrations of toxic phytoplankton. This, in essence, is the situation proposed by Hardy in his theory of "animal exclusion."

Summary

1. The filtering rate of *Daphnia magna,* defined as the volume of water swept free of food per animal per unit of time, was determined from one-hour feeding experiments using as food organisms the Chlorophyta *Chlorella vulgaris* and *Scenedesmus quadricauda* and the diatom *Navicula pelliculosa.*

2. Filtering rate per unit of weight of *Daphnia* is an inverse function of the animal's size. Under given conditions, the maximum filtering rate occurs in animals approximately 2.7 mm. in length.

3. Starved *Daphnia* feed upon *Chlorella* at the same rate as animals which had previously fed upon bacteria and detritus and whose intestines were filled with such material at the onset of the experiments.

4. The filtering rate of *Daphnia* is inhibited by substances produced by the three species of algae tested. The inhibitory product of *Chlorella* appears to be identical to the previously described antibiotic, chlorellin. The inhibition is mediated partially by substances which diffuse from the cells and accumulate in the water. A much more pronounced effect appears to be produced by the release of the inhibitory products from ingested cells within the animal.

5. The minimum inhibition is produced by actively growing algae from cultures which are in their log phase of growth. The maximum effect is produced by senescent, non-dividing algae.

6. In the one-hour feeding experiments in which starved or bacteria-and-detritus-fed *Daphnia* were fed varying concentrations of the algae, the filtering rate was inversely proportional to the concentration of cells in the water. The explanation was proposed that the filtering rate is proportional to the rate of ingestion of cells and assimilation of their inhibitory products, both of which in these experiments were dependent upon the concentration of cells in the water.

7. When *Daphnia* were fed actively growing *Chlorella* for 12 hours prior to the feeding experiments, the filtering rate for the ensuing one-hour period was much lower than that of starved

Daphnia at any given concentration of the algae. At *Chlorella* concentrations below 0.15 million cells per ml. the filtering rate was inversely proportional to the concentration of the algae. At concentrations above that value the filtering rate was constant.

8. No sign of feeding could be detected in *Daphnia* which had been exposed to suspensions of senescent, non-dividing *Chlorella* for periods of 12 hours prior to the feeding experiments.

9. Within the size range represented by *Chlorella* (3.6 μ^3) and *Scenedesmus* (25.5 μ^3) *Daphnia* shows no selectivity in its feeding, removing cells of both species at the same rate from mixed populations of these algae.

10. *Daphnia* cultured upon actively growing *Chlorella* cells grew rapidly and, upon reaching maturity, maintained a high rate of reproduction. *Daphnia* cultured upon senescent, non-dividing *Chlorella* grew very slowly, failed to reproduce, and died after 11-13 days.

11. The possibility and ecological significance were discussed of a widespread occurrence in nature of the inhibition of zooplankton filter feeders by senescent populations of phytoplankton. This relationship was proposed as a physiological basis of Hardy's theory of "animal exclusion."

References

Allison, J. B., and W. H. Cole. 1934. Note on the behavior of the barnacle. Bull. Mt. Desert Biol. Lab., 1934.

———. 1935. Behavior of the barnacle, *Balanus balanoides,* as correlated with the planktonic content of sea water. Bull. Mt. Desert Biol. Lab., 1935.

Bückmann, A. 1934. Shellfish. Rapp. Cons. Explor. Mer, **94**(2): 39.

Fleming, R. H. 1939. The control of diatom populations by grazing. J. Cons. int. Explor. Mer, **14**: 1-20.

Fuller, J. T. 1937. Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. Biol. Bull., **72**: 233-246.

———, **and G. L. Clarke.** 1936. Further experiments on the feeding of *Calanus finmarchicus.* Biol. Bull., **70**: 308-320.

Gauld, D. T. 1951. The grazing rate of planktonic copepods. J. Mar. Biol. Assoc. U. K., **29**: 695-706.

Hardy, A. C., and E. R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. Discovery Reports, **11**: 1-456.

Hardy, A. C. 1936. The ecological relations between the herring and the plankton investigated with the plankton indicator. J. Mar. Biol. Ass. U. K., **21**: 147-177.

Harvey, H. W. 1937. Note on selective feeding by *Calanus.* J. Mar. Biol. Ass. U. K., **22**: 97-100.

———. 1942. Production of life in the sea. Biol. Rev., **17**: 221-246.

———, **L. H. N. Cooper, M. V. Lebour and F. S. Russell.** 1935. Plankton production and its control. J. Mar. Biol. Ass. U. K., **20**: 407-442.

Hoagland, D. R., and W. C. Snyder. 1933. Nutrition of strawberry plant under controlled conditions. Proc. Amer. Soc. Hort. Sci., **30**: 288-294.

Korringa, P. 1950. A review of the papers on molluscs presented at the special scientific meeting on shellfish of the International Council for the Exploration of the Sea, Edinburgh, 10th October 1949. J. Cons. Int. Explor. Mer, **42**: 44-59.

Lefèvre, M., H. Jakob and M. Nisbet. 1951. Compatibilités et antagonismes entre algues d'eau douce dans les collections d'eau naturelles. Trav. Assoc. Internat. Limn. theor. et appl., **11**: 224-229.

Loosanoff, V. L., and J. B. Engle. 1947. Effect of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). Bull. U. S. Bur. Fish., **51**: 31-57.

Lucas, C. E. 1936. On certain inter-relations between phytoplankton and zooplankton under experimental conditions. J. Cons. int. Explor. Mer, **11**: 343-362.

———. 1938. Some aspects of integration in plankton communities. J. Cons. int. Explor. Mer, **13**: 309-322.

———. 1947. The ecological effects of external metabolites. Biol. Rev., **22**: 270-295.

———. 1949. External metabolites and ecological adaptation. Symp. Soc. Exp. Biol. III; Selective toxicity and antibiotics: pp. 336-356. New York: Academic Press.

Nightingale, H. W. 1936. Red water organisms—their occurrence and influence upon marine aquatic animals with special reference to shellfish in waters of the Pacific coast. Seattle: Argus Press.

Marshall, S., A. G. Nicholls, and A. P. Orr. 1935. Biology of *Calanus finmarchicus.* VI. Oxygen consumption in relation to environmental conditions. J. Mar. Biol. Assoc. U. K., **20**: 1-27.

Otterström, C. V. and E. Steemann Nielsen. 1939. Two cases of extensive mortality in fishes caused by the flagellate, *Prymnesium parvum,* Carter. Rep. Danish Biol. Sta., **44**: 6-24.

Pennak, R. W. 1946. The dynamics of freshwater plankton populations. Ecol. Monogr., **16**: 339-356.

Pratt, R., and J. Fong. 1940. Studies on *Chlorella vulgaris.* II. Further evidence that *Chlorella* cells form a growth inhibiting substance. Amer. J. Bot., **27**: 431-436.

———, **et al.** 1944. Chlorellin, an antibacterial substance from *Chlorella.* Science, **99**: 351-352.

Pratt, R., J. F. Oneto, and J. Pratt. 1945. Studies on *Chlorella vulgaris.* X. Influence of the age of the culture on the accumulation of chlorellin. Amer. J. Bot., **32**: 405-408.

Raymont, J. E. G., and F. Gross. 1942. On the feeding and breeding of *Calanus finmarchicus* under laboratory conditions. Proc. Roy. Soc. Edinb., **61**: 267-287.

Rice, T. R. 1954. Biotic influences affecting population growth of planktonic algae. U. S. Fish & Wild. Serv. Fish. Bull. **54** 227-245.

Riley, G. A. 1946. Factors controlling phytoplankton populations on Georges Bank. J. Mar. Res., **6**: 54-73.

———. 1947. A theoretical analysis of the zooplankton population of Georges Bank. J. Mar. Res., **6**: 104-113.

Scott, G. T. 1943. The mineral composition of *Chlorella pyrenoidosa* grown in culture media containing varying concentrations of calcium, magnesium, potassium, and sodium. J. Cell. and Comp. Physiol., **21**: 327-338.

Storey, J. 1943. [Quoted from 11th annual report, Freshwater Biol. Assoc. Brit. Emp.: pp. 17-18.]

AN UPLAND FOREST SURVEY OF THE MILWAUKEE AREA[1]

PHILIP B. WHITFORD AND PETER J. SALAMUN
University of Wisconsin Extension Division, Milwaukee, Wisconsin and Wisconsin State College, Milwaukee, Wisconsin

In common with the expansion of urban centers all over the country, Milwaukee has experienced a period of great expansion and is rapidly overrunning the remnants of the once rich flora which characterized the county. A floristic report on Milwaukee County including much historical data was written by Shinners (1940). This thesis reviewed the numerous reports of early floristic botanists such as I. A. Lapham, T. A. Bruhin, W. M. Wheeler, and E. Bruncken. None of these men, however, seems to have collected quantitative data. In view of this fact, it seemed desirable to obtain a detailed picture of the relationships among the species in the Milwaukee area, and to make a quantitative record of the forest stands remaining in the locality.

DESCRIPTION OF THE AREA

Tension zones among three major types of vegetation converge in Milwaukee County (see Fig. 1). The prairie peninsula, or grassland formation, which covers large areas in southern Wisconsin, touches Lake Michigan not far to the south and to a large extent separates the forests bordering the lake to the north of Chicago from the forests approaching the lake from the east and south (see map of the prairie peninsula in Lindsay 1953). The deciduous forest, typical of much of Wisconsin, furnishes the predominant native vegetation type near Milwaukee. The mixed conifer-hardwood forest, or "Lake Forest," appears in scattered relict stands along the lake shore, resulting in a number of more northern tree and understory species within the ravines in the northeastern corner of the county. In addition to the convergence of these major types, there is also the problem of the range of beech (*Fagus grandifolia*),[2] which extends through Milwaukee County along the lake but is limited to the eastern and northern portions of the county.

Milwaukee County is located in the southeastern part of Wisconsin, on the west shore of Lake Michigan. For the purposes of this study an arbitrary limit of fifteen miles radius from the mouth of the Milwaukee River was established as the boundary of the field work because some areas of the county have been so greatly disturbed that it was necessary to go a short distance beyond the county limits to find woods in sufficiently good condition to repay the effort of collecting data.

The area of the study lies entirely on glacial drift, chiefly of the third Wisconsin substage; although some red drift of the fourth Wisconsin substage occurs along the lake shore in the northeastern portion. The resultant topography consists of a gently undulating series of three moraines which are generally parallel to the lake shore. The main streams of the area follow the valleys between the moraines (Alden 1918). The Milwaukee River flows southward through the northeastern portion of the county and is joined by the Menominee, which drains the northwest and central portions, just before it enters the lake in the east center of the county. In the southwest, the drainage is through the Root River, which flows southeastward and enters the lake in Racine County. The southeastern part of the county is drained by two small streams which empty directly into Lake Michigan.

The soils of the area are chiefly clay loams of the Miami series except those on the red drift which are of the Superior series (Whitson *et al.* 1919).

Milwaukee County lies in the transition zone between climatic regions I and IV of Borchert (1950), or in the fluctuating limits of the Da/Db

[1] The field study reported in this paper was supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation. Our sincere appreciation is due also to Dr. J. T. Curtis and to Mrs. Philip Whitford for helpful advice and criticism of the manuscript.

[2] Taxonomic nomenclature in this paper follows Fernald (1950).

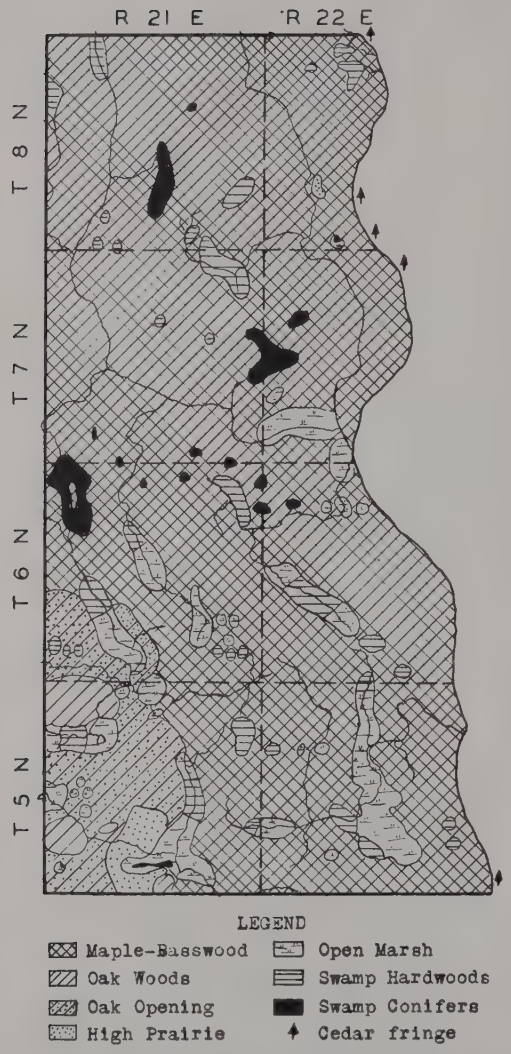

FIG. 1. Map of Milwaukee County showing the original vegetation as taken from land survey records of 1835-36 (based on a map plotted by Mr. H. Klahorst).

boundary of Köppen (Villmow 1952). A climatic summary for Milwaukee (U. S. Weather Bureau 1953) indicates that the average annual temperature is 46.6° F. Means for the warmest and coldest months, July and January respectively, are 70.9° F. and 21.4° F. The average annual precipitation is about 30 inches, of which two-thirds occurs during the growing season. Prevailing winds are westerly or southwesterly in the summer, and northwesterly or northeasterly in the winter.

These data, however, do not readily reflect the variations in climate existing within the county. The influence of Lake Michigan is of particular significance. During the spring and summer months a sudden shift of the wind to an easterly or southeasterly direction is frequently accompanied by a sudden drop of ten or fifteen degrees in temperature. In the autumn, the relatively warm water of the lake prevents nighttime temperatures from falling so low as they do several miles inland. The full influence of the lake is most apparent immediately along the shore, particularly in the ravines entering it. Cooler summer temperatures with accompanying higher humidities and more persistent winter snow cover in these locales enable species of the coniferous forest to persist. Farther inland warmer summer temperatures accompanied by lower humidities and less persistent winter snow cover favor deciduous forest and, to a limited extent, prairie species. Microclimates formed by local slopes, exposures and changes of drainage further complicate the climatic pattern within the county.

METHODS

In 1951, a field survey of 22 upland forest stands was conducted using the "random pairs" method established by Cottam and Curtis (1949). This method has been used at the University of Wisconsin Ecology Laboratory in the field study which resulted in the "continuum theory" of vegetation (Curtis and McIntosh 1951). The stands selected for this study were those over five acres in extent which showed the least possible degree of disturbance, although, in the history of the urban development here, most of them must have been subjected to some grazing or cutting in the past.

The field data for trees of the present study were computed in terms of the continuum index values for each stand in order to relate them to the statistical scale representing transition from "initial stages" to the "terminal stage" of the Wisconsin hardwood forest in general. The arbitrary scale of the continuum as defined by Curtis and McIntosh is based on the importance value (I.V. equals the sum of relative frequency, relative density, and relative dominance) of each species in a stand (300 total points) multiplied by a "climax adaptation number" (C.A.N.) ranging from 1 to 10; thus the scale has values from 300 representing a pure stand of very intolerant trees such as bur oak (*Quercus macrocarpa*), to 3000 which would represent a pure stand of very tolerant trees such as sugar maple (*Acer saccharum*.)

In an effort to clarify the geographical transition from initial to terminal forest types, the con-

tinuum values of the stands were plotted on a map and "contour lines" were drawn at intervals of 200 units on the continuum scale (Fig. 3).

Understory data were evaluated in terms of the continuum by use of the method of Gilbert and Curtis (1953) which is based on the presence of selected species in five groups. The presence values of this system, which has a scale from 100 to 500, were then converted to the same scale as the tree data by the formula

$$C = [(P - 100) \times 6.75] + 300,$$

where C is the continuum index value and P is the presence index value.

Saplings are also tallied in the field to complete the understory data, and a sapling continuum value for each stand was computed for comparison with the values derived from trees 4 inches in diameter and over. Since the sapling data did not include dominance values, the importance values were calculated using the formula

I.V. = relative density + relative frequency $\times$ 1.5.

The resultant values compare directly to the importance values (I.V.) for trees which were based on relative dominance, relative density and relative frequency.

The comparisons of herb and shrub continuum values with those of the trees, and of saplings with larger trees, were graphed and computed mathematically by using Pearson's formula (Gavett 1937) for linear correlation

$$r = \frac{\Sigma x'y' - Nx'y'}{N\sigma x\sigma y}.$$

The data are shown on scatter diagrams in Figures 5 and 6.

Results and Discussion

Tree data

Table I summarizes the field data. This table shows the importance values of each tree species in each of the 22 stands (species recorded in the frequency data for only one stand are omitted). The stands are here arranged in continuum order, and continuum index values are included below. Climax adaptation numbers of each species, as well as total importance values of each for all areas sampled, are included in the table for easy comparison. Note that white oak (*Quercus alba*) shows far higher values in the first half of the continuum, while sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*), as would be expected, show highest values in the latter half of the scale. Red oak (*Quercus rubra*), and to a lesser degree white ash (*Fraxinus americana*), show highest values in the central range. Ironwood (*Ostrya virginiana*) seems to be ubiquitous as an understory tree but, like basswood (*Tilia americana*), has a somewhat higher trend toward the later stages of the continuum.

The dominant species show the same general relationships as in the broader study by Curtis and McIntosh except that in the Milwaukee area white oak (*Q. alba*) was found to be first and red oak (*Q. rubra*) third in over-all importance; while Curtis and McIntosh found them to be, respec-

Table I. *Importance values of the major tree species found in 22 stands in the Milwaukee area*

C.A.N.*	Species	Importance values (I. V.)																					Total (I. V.)
10.0	*Acer saccharum*		38		19	35	57	20	58	12	85	65	113	57	48	53	66	58	71	44	101	68	127	1196
10.0	*Fagus grandifolia*													16		19	21		29	78	21	164	74	431
9.0	*Ostrya virginiana*	8	3	3	18	12	29	16	24	28	21	3	9	12	23	26	24	54	6	14	15	4	22	372
8.5	*Carya cordiformis*				3					3	3												4	13
8.0	*Tilia americana*		5	13	27	57	25	18	8	7	32	19	6	63	35	19	4	44	42	47	73	14	6	561
8.0	*Ulmus fulva*	4		30	10		15	42	6	32		3	14	13	49		7	20	68	13		4	13	341
7.5	*Fraxinus americana*		6	12	16	13	6	28	12	5	20	22	6	3	15	5	30	17	20	22	6	10	9	281
7.0	*Acer rubrum*	4	12		14				10	57		6	19				14	17		5			4	158
7.0	*Juglans cinerea*																4			11		4	10	29
7.0	*Ulmus americana*	31	3	39	3	21	6	4	39	17		29			10		11	23	4	12			16	267
6.0	*Fraxinus nigra*										3					16								19
6.0	*Quercus rubra*	60	40	58	33	6	23	97	29	97	28	95	22	22	71	13	81	37	22	29	34			898
5.0	*Betula papyrifera*													28		76					36	4		145
5.0	*Juglans nigra*	4		12			8						4		10				4					42
5.0	*Pinus strobus*													68							8			76
4.0	*Quercus alba*	135	173	94	140	142	126	44	73	38	95	53	101		36		30	26	20	7				1331
3.5	*Carya ovata*	16	8				6		19			3		4	4								13	73
3.5	*Prunus serotina*	13		3	12	9			3				7	3			3		4	3		29		89
2.0	*Quercus ellipsoidalis*	27		7																				34
2.0	*Crataegus* spp.			11	6				3		12	3						4	6	3			3	51
1.5	*Populus grandidentata*															5	5							10
1.0	*Quercus macrocarpa*		12	18		6		23		6	3			8										76
Continuum index values		1428	1564	1583	1717	1797	1917	1930	1951	1996	2002	2052	2098	2109	2170	2225	2227	2330	2386	2398	2424	2710	2712	
Stand number		15	2	14	4	1	11	17	13	3	7	22	6	10	8	21	5	16	18	19	9	20	12	

*Climax adaptation numbers (after Curtis and McIntosh 1950).

tively, third and first in order of importance. Beech (*F. grandifolia*), which was lacking in the earlier study, is important in Milwaukee County. It should also be stated that some of the tree species found here were absent or only rarely present in the area studied by Curtis and McIntosh; therefore climax adaptation numbers for these had to be either taken from the northern forest continuum of Brown and Curtis (1952) or interpolated according to the apparent behavior of each in the Milwaukee area. This may result in some distortion of continuum values, but since this area lies within a tension zone this compromise seems to be the best which can be obtained for the present.

The ten leading species in over-all importance values are, in descending order: white oak (*Quercus alba*), sugar maple (*Acer saccharum*), red oak (*Q. rubra*), basswood (*Tilia americana*), beech (*Fagus grandifolia*), ironwood (*Ostrya virginiana*), slippery elm (*Ulmus rubra*) ash (*Fraxinus* spp.), white elm (*U. americana*), and red maple (*A. rubrum*). The first three species in importance values together represent over ½ the total value of all the trees tabulated.

In the Milwaukee area, the actual values of the stands range from 1428 to 2712. This indicates that only the upper two-thirds of the continuum scale is represented here. Stands in the area studied by Curtis and McIntosh had values from 632 to 2650. Although native prairie appears in the southwest corner of the county, the very intolerant species like black oak (*Quercus velutina*) and bur oak (*Q. macrocarpa*) which typify the prairie border occur, at least in the present remnants, only as a few scattered trees. The open oak stands, as one might expect, were very limited in extent, and were, as the land records show, the favorite locations of the pioneer land seekers (Schafer 1927). The open oak stands which escaped early destruction were few in number and of those remaining some may already have been converted by the advent of more tolerant species. One stand recorded in this study (Fig. 6) which was described by the surveyors in 1835-1836 as "oak opening" now shows scattered open grown trees interspersed with many smaller trees.

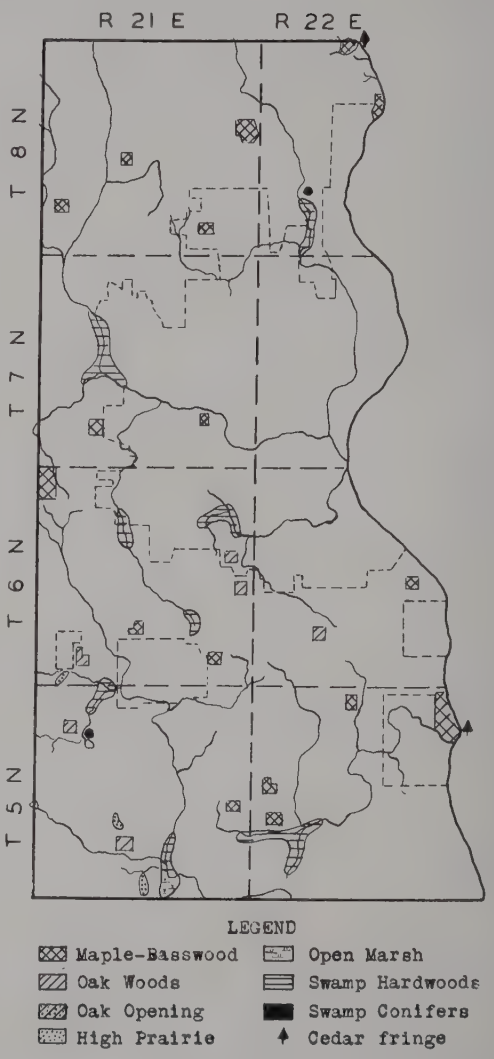

FIG. 2. Map of Milwaukee County as of 1951, showing incorporated areas of the city of Milwaukee and its suburbs together with the existing native vegetation as checked during the present study.

Continuum contours

The map of continuum values (Fig. 3) shows that most of the low values, as expected, appear in the southwest corner, while high values are found across the north end and along the lake shore. However, two areas of lower values extend toward the lake in the central and north central portions. It is assumed that these result from tongues of drier, warmer air masses carried by prevailing westerly winds or, conversely, that the westward extension of high values is due to favorable climatic conditions resulting from channels of cooler, moister air flowing from the lake. These "lake breezes," which frequently occur in the summer, are an obvious and probably important part of the local climate, and commonly bring a rapid fall of temperature in a matter of minutes, with an accompanying rise in relative humidity. Undoubtedly, this frequent reduction of transpiration stress

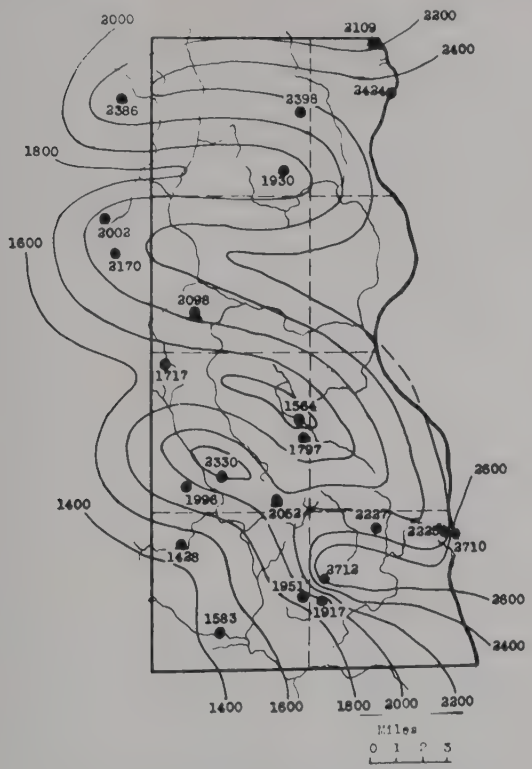

FIG. 3. Map of Milwaukee County showing locations of stands (dots) and their continuum index values. The superimposed lines represent "contours" of these values at 200 unit intervals.

by midafternoon of hot, dry summer days could prevent fatal wilting of seedlings of the more mesic species during this otherwise critical period.

Unfortunately, the intensive development of the city and its suburbs prevented the finding of any reasonably undisturbed stands in the east-central part of the county. However, observations by the authors of the native trees remaining in county parks and other places (Fig. 2) show that oaks extend well to the east in line with the easterly lobes of low continuum values, while sugar maple (*Acer saccharum*) is common westward to the county line in the area between these lobes.

The continuum index values of the two stands in the extreme northeast part of the county are rather low considering that sugar maple (*A. saccharum*) and beech (*Fagus grandifolia*) are important species. These lower values are probably due to the presence of such northern species as white pine (*Pinus strobus*) and paper birch (*Betula papyrifera*). The climax adaptation numbers of these northern species were taken from the scale devised for the conifer-hardwood forest continuum by Brown and Curtis (1952). It is probable that this scale is not comparable to the one used for the prairie-forest border continuum.

Distribution of beech

The distribution of beech (*F. grandifolia*) in Wisconsin is another problem of interest here because its western limit tapers out from the northwestern corner to the southeastern corner of the county, ending with a few stands near the lake in the next county southward. Northward this range gradually widens from the lake to include the Green Bay area and a considerable portion of northeastern Wisconsin. Shanks (1953) found that in Ohio the beech is favored by heavy, poorly aerated soils and develops almost pure stands on such sites while lighter or better drained and aerated soils on slopes were favorable for sugar maple (*Acer saccharum*) and resulted in mixed beech-maple stands.

Ward (1953) discussed the nature of the beech border in Wisconsin and concluded that fire was not an important factor, but that soil or climate or a combination of these must limit its range. Camp (1953) discussed the distribution of this species in eastern North America with reference to its subspecific variations, and concluded that its western limit seems to coincide with the line of 30 inches of annual rainfall. Milwaukee County is just within this limit.

Another hypothesis is that the range of beech is still being gradually extended, or has extended somewhat within the past two centuries. Most of the trees here are relatively small, especially in the westernmost stands. At this extreme edge of its range it seems to follow stream valleys and is confined to the Lake Michigan drainage system which in this area is within 10-15 miles of the lake. Apparently it has not entered the watersheds of the Des Plaines or Fox Rivers which drain southward into the Illinois and Mississippi Rivers from headwaters approaching Milwaukee County on the south and west respectively.

Whether this distribution pattern is more a result of soil moisture, climate, or migration is a moot question; the facts may be merely coincidental.

Saplings

Theoretically, the sapling layer of a forest stand should be composed of more tolerant species than the canopy layer, except in the terminal stage where they are the same. This was tested by using the sapling data to compute a sapling continuum, as described under methods, and comparing this with the continuum values of each stand on a scatter diagram (Fig. 4). This diagram shows that the theory holds true for most stands,

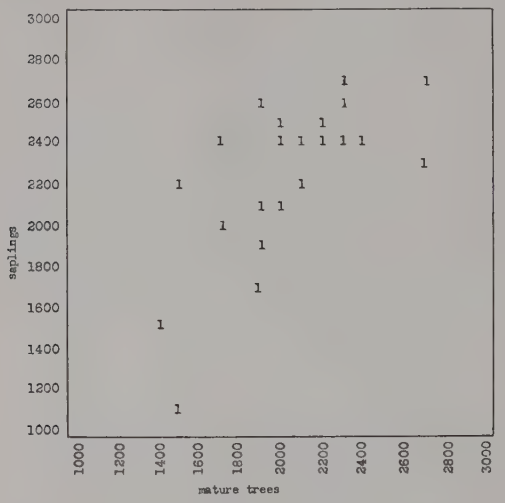

FIG. 4. A comparison of sapling continuum index values of 22 stands with the continuum index values for trees over 4 inches d.b.h.

for the sapling continuum index values are usually higher than are the values for the larger trees. Using Pearson's formula, the linear correlation between trees and saplings was computed to be .67 ± .08, which indicates a significant correlation between these two sets of values. The few cases in which sapling values are lower than expected may be the result of selective cutting at some time in the past history of those stands or of wind damage opening up some stands sufficiently for the growth of less tolerant species.

Understory

The understory species of forest stands normally show a tendency to respond to the controlling canopy, and to the competition of the dominant species. This tendency seems to be correlated with the forest continuum as shown by Curtis and McIntosh (1951) in their graphs of selected species, and by Gilbert and Curtis (1953) in their paper on the herb continuum. However, the herb continuum based on presence, as used in the latter paper, when applied to the stands in the Milwaukee area, shows a poor correlation with the tree continuum. The scatter diagram in Figure 5 shows no significant relationship in this area. A mathematical comparison using Pearson's formula, in this case $r = .40 \pm .12$, further suggests only a slight correlation. This poor correlation may result in part from the unsuitability of indicator species from the statewide study for use in this limited area which is a tension zone. Such an unsuitability of the statewide indicator species would, however, only serve to point out further the divergences between this area and that extending farther westward in the state. It is also logical to assume that the proximity of seed sources from a broad range of forest types should lead to at least the occasional establishment of species in local areas within stands of types other than those in which they normally occur. Presumably such establishment would lead to relatively high average presence values for many understory species and result in a poorer correlation value. This seems to be true in Milwaukee County.

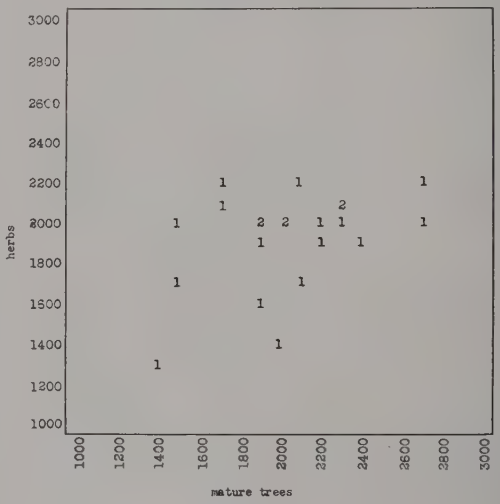

FIG. 5. A comparison of herb continuum index values of 22 stands with the continuum index values of trees.

The frequency data for herbs and shrubs indicated that 43 species occurred in quadrats in at least ½ of the stands. Presence lists included 61 species which occurred in ½ or more of the stands sampled. Average frequency and presence values were tabulated for the common herbs, and the ten having the highest average frequency values are listed in Table II.

TABLE II. *Average frequency (%) and presence (%) of the ten most common herbs*

Species	%F	%P
1. *Geranium maculatum*	46.8	95.5
2. *Claytonia virginica*	32.8	77.3
3. *Smilacina racemosa*	28.4	100.0
4. *Circaea quadrisulcata*	26.3	90.9
5. *Viola pubescens*	23.2	90.9
6. *Osmorhiza claytoni*	20.9	63.6
7. *Anemone quinquefolia*	20.2	95.5
8. *Viola cucullata*	20.0	90.9
9. *Trillium grandiflorum*	18.7	100.0
10. *Hepatica acutiloba*	18.6	72.7

Five species were present in all 22 stands: wild leek (*Allium tricoccum*), jack-in-the-pulpit (*Arisaema atrorubens*), avens (*Geum canadense*), false spikenard (*Smilacina racemosa*), and the large-flowered trillium (*Trillium grandiflorum*). Four others were present in all but one stand: wood anemone (*Anemone quinquefolia*), cranesbill (*Geranium maculatum*), poison ivy (*Rhus radicans*), and choke cherry (*Prunus virginiana*). These are the commonest species in terms of wide ecological distribution, but they are not necessarily high in frequency or numbers in the average stand. Frequency values are affected by the size and growth habits of each species, a fact which must be kept in mind in any direct comparison of frequencies (Whitford 1949). Of the species listed above, the cranesbill (*Geranium maculatum*) with 95.5% presence has an average frequency of 46.8%, the highest found in this study, while the wild leek (*Allium tricoccum*) which has a presence of 100% has an average frequency of only 8.8%. The second highest average frequency was that of the spring beauty (*Claytonia virginica*) with 32.8%. All the other species averaged less than 30% although some of them were locally abundant.

Northern species

The occurrence of species which are more commonly found farther north, and which at this latitude in Wisconsin are restricted to local favorable areas, is worthy of note. Yellow birch (*Betula lutea*) and white cedar (*Thuja occidentalis*) are two such representatives, both occurring in ravines along the lake. Two other northern species were recorded in some of the stands studied. White pine (*Pinus strobus*) was listed in two of the stands, and white birch (*Betula papyrifera*) in four; the latter species is rather common along the lake shore in the northeast part of the county.

Several shrubs and herbs with boreal affinities were also noted in some of the stands. Soapberry (*Shepherdia canadensis*) and yew (*Taxus canadensis*) were found in the extreme northeastern stand. The star flower (*Trientalis borealis*) was found in two stands and the red-berried elder (*Sambucus pubens*) in one. Some of these spe-

Fig. 6. Interior view of Stand No. 14, continuum index value 1583. Note the open-grown white oak surrounded by younger white and red oak, slippery elm, etc.

Fig. 7. Interior view of Stand No. 20, continuum index value 2710. This stand had the highest proportion of beech among those studied and was located within ¼ mile of the lake in the southeastern part of the county.

cies, together with such other northern ones as twin flower (*Linnaea borealis*), wintergreen (*Gaultheria procumbens*), gold-thread (*Coptis trifolia*), and blueberries (*Vaccinium* spp.), were recorded before 1900 from bogs which long since have been drained or filled (Russel 1907 and Shinners 1940). The influence of Lake Michigan on the persistence of these northern species is apparent when one considers its effect on the degree and duration of maximum summer temperatures as noted in the climatic summary. Further effects of the lake which may be important here are: the tree buds open later in the spring; the first killing frost is delayed in the fall; and the snow cover is more persistent during the winter, particularly on the north and northeast exposures of ravines, with the result that there is probably less frost heaving.

Summary

1. A survey of 22 upland forest stands was made using the "random pairs" method of sampling. The data were analyzed in terms of the continuum concept.

2. The remnant stands in this area are chiefly mixed hardwoods with white oak (*Quercus alba*), sugar maple (*Acer saccharum*) and red oak (*Q. rubra*) making up over one-half of the total tree species. Continuum index values of these stands range from 1428 to 2712. These values represent the upper two-thirds of the continuum scale.

3. Continuum values were determined for the saplings and a comparison was made with those for the trees. Saplings correlated very well with the trees but, in general, had higher continuum values in each stand.

4. Herb continuum values were also computed. These, however, correlated poorly with the trees, indicating that perhaps there may be more mixing of types in the understory here than is usual in the centers of floristic regions.

5. Several species of a more northern distribution occur here, especially in the ravines near Lake Michigan.

References

Alden, W. C. 1918. The quaternary geology of southeastern Wisconsin. U. S. Geol. Surv. Prof. Paper **106**.

Borchert, John R. 1950. The climate of the central North American grassland. Ann. Assoc. Amer. Geog. **40**: 1-39.

Brown, R. T., and J. T. Curtis. 1952. The upland conifer hardwood forests of northern Wisconsin. Ecological Monog. **22**: 217-234.

Camp, W. H. 1953. The beech *Fagus* population in North America. Paper presented before the American Society of Plant Taxonomists, Madison, Wisc., September, 1953.

Cottam, Grant, and J. T. Curtis. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology **30**: 101-104.

Curtis, J. T., and R. P. McIntosh. 1950. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32**: 476-496.

Fernald, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., New York.

Gavett, G. I. 1937. A first course in statistical method. McGraw-Hill Book Co., Inc., New York.

Gilbert, M. L., and J. T. Curtis. 1953. Relation of the understory to the upland forest in the prairie-forest border region of Wisconsin. Wisc. Acad. Sci., Arts, Letters. Trans. **42**: 183-185.

Lindsay, D. R. 1953. Climate as a factor influencing the mass ranges of weeds. Ecology **34**: 308-321.

Russel, H. 1907. Check list of the flora of Milwaukee County. Bull. Wisc. Nat. Hist. Soc. **5**: 167-250.

Schafer, Joseph. 1927. Four Wisconsin counties. State Hist. Soc. Wisc., Madison, Wisc.

Shanks, R. E. 1953. Forest composition and species association in the beech-maple forest region of western Ohio. Ecology **34**: 455-466.

Shinners, L. H. 1940. The vegetation of the Milwaukee region. Bachelor's thesis, Univ. Wisc., Madison.

U. S. Weather Bureau. 1953. Local climatological data 1952, Milwaukee, Wisconsin. Govt. Printing Office, Wash., D. C.

Villmow, J. R. 1952. The position of the Köppen Da/Db boundary in eastern United States. Ann. Assoc. Amer. Geog. **42**: 94-97.

Ward, R. T. 1953. The nature of the beech border in southern Wisconsin. Paper presented before the Ecological Society of America, Madison, Wisc., Sept., 1953.

Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth: Ecology **30**: 199-208.

Whitson, A. R. 1927. Soils of Wisconsin. Wisc. Geol. and Nat. Hist. Surv. Bull. No. **68**. Soil Series **49**.

Whitson, A. R., W. J. Geib, and T. J. Dunnewald. 1919. Soil survey of Milwaukee County, Wisconsin. Wisc. Geol. and Nat. Hist. Surv. Bull. No. **56A**. Soil Series No. **28**.

NOTES ON THE ECOLOGY OF THE MIDGE FAUNA (DIPTERA: TENDIPEDIDAE) OF HUNT CREEK, MONTMORENCY COUNTY, MICHIGAN

La Verne L. Curry[1]
Central Michigan College of Education, Mount Pleasant, Michigan

Although invertebrate organisms inhabiting trout streams have long been recognized as important items of fish food, little is known regarding the genera and species of the true nematocerous midges. In the past, reports covering investigations on Michigan trout streams listed many immature forms of insects identified to genus and species. However, when considering the Tendipedidae (= Chironomidae), the family usually was divided into groups and the individual forms listed numerically. This method was employed because of insufficient knowledge of the taxonomy within the group, especially of immature stages.

During the summer of 1952 a preliminary investigation of the family was conducted along Hunt Creek (T.29 N., R.2.E., Sections 25, 34, 35, 36) Montmorency County, Michigan. The work was undertaken to determine the specific midge fauna of the stream in the vicinity of Hunt Creek Experiment Station, to collect information regarding the morphology and life history of the various species collected, and if possible to obtain data regarding the ecological relationships existing between the various members of the fauna and the stream bottom as determined by the plant associations of the adjacent stream valley.

The portion of stream studied was approximately two miles long and flowed in a general northeasterly direction through state-owned land. The terrain within this section (roughly three square miles) was such that four distinct ecological situations were recognized. They were: beaver dam impoundments; highlands; black spruce-white cedar-tamarack swamp; and sedge-meadow (marsh).

Description of Areas Studied

Hunt Creek holds a unique place among Michigan's smaller trout streams in that the brook trout (*Salvelinus fontinalis fontinalis*) is able to maintain a fairly large population within its waters. The stream is essentially spring-fed, and is not generally subject to flooding unless a beaver dam washes out, or an excessively heavy rain occurs. The stream receives comparatively little runoff water.

[1] Contribution from Michigan Institute for Fisheries Research.

Due to the origin of the water within the stream, its temperature remains cold in summer, dropping into the low fifties at night even during the hottest part of the summer. During the winter the stream remains open throughout a major portion of its length in the experimental area. The beaver ponds and portions of Section "A" (Fig. 1) freeze over in winter. Throughout the area trout display a slow growth rate as compared to those from such streams as the Pigeon and north branch of the Au Sable.

The soil of the "highlands" is composed of morainic materials, sand and gravel, while that of the drainage basin is in general thin, light, and poor.

The portion of Hunt Creek flowing within the area of state-owned land has been divided into sections to facilitate the study of creel-census reports. The sections are designated as "Z," "A," "B," "C," and "D" starting at the downstream portion of the controlled area and extending upstream toward the headwaters (Fig. 1). Concrete weirs containing self-cleaning rotary screens have been installed in the stream at the junction of Sections "C" and "D," and at the lower limits of Section "Z". The weirs enable the staff at the station to study the migratory habits of the trout within the stream.

Portions of the stream investigated have been described by Leonard (1940, 1942a, b), Shetter and Leonard (1943), and Shetter, Clark, and Hazzard (1949). For convenience a summary of the four ecological areas is given from these researches. The botton deposits recorded during this investigation are based on Roelof's (1944) classification of lake muds.

The beaver impoundments located in Section "D" (Fig. 1) occurred in the upper reaches of the stream and were bordered by two types of vegetation. The ponds proper were located in the center of a wide sedge-meadow rimmed with a sparse growth of aspen on the higher ground. The ponds were open and had no discernible current even where the stream had narrowed to a width of several feet. Toward the headwaters of the stream the meadow narrowed abruptly and was replaced by a white cedar-tamarack swamp. The bottom deposit of the standing waters within these areas was mainly muck and detritus. Sta-

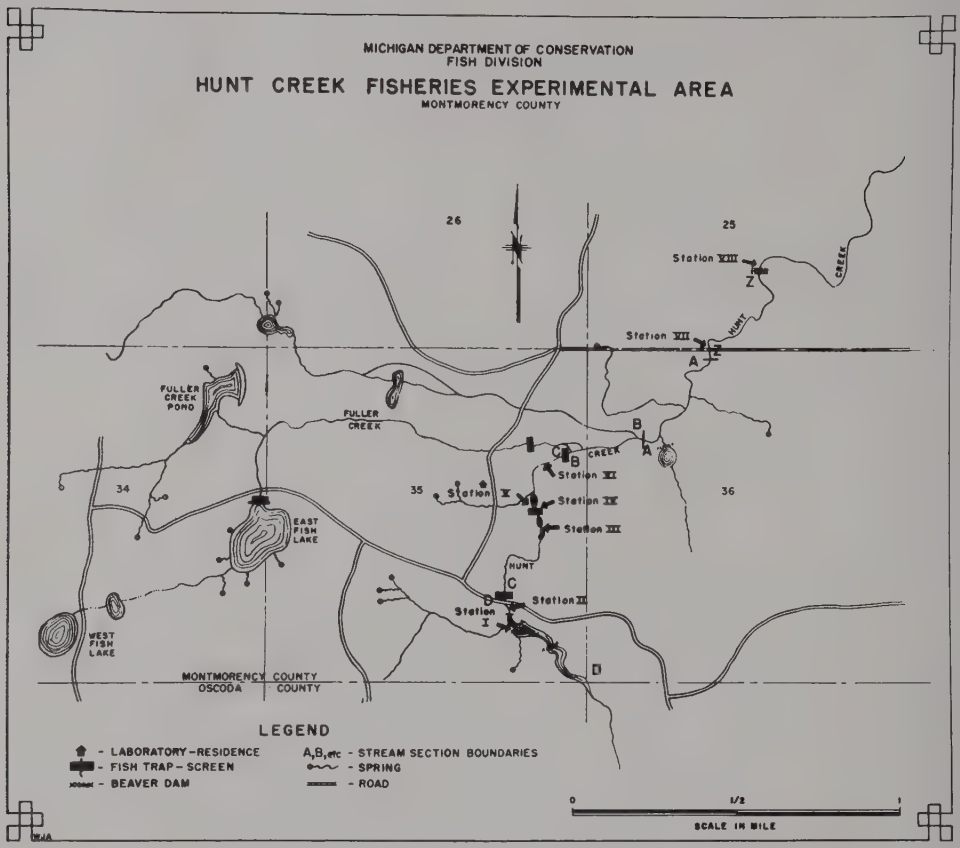

FIG. 1. Map of Hunt Creek experimental area.

tion 1 was established in a pool at the foot of the largest beaver dam (Fig. 1). The dam was approximately 75 feet long and impounded the water above the dam to a depth of about five feet above the water in the stream below. The stream directly below the dam ranged from 15-20 feet in width, narrowing rapidly downstream to about 10 feet. The pool in which Station 1 was established was about 4 feet deep, but, while collections were being made at this site during the fall, the beaver constructed a new dam downstream and increased the depth of water to almost 5 feet.

Station 2 was also established in Section "D" (Fig. 1) directly below an old wooden bulkhead constructed by the CCC as a stream-improvement structure. The stream at this point was typical of that found in the "highlands," being about six feet wide with a swift current and flowing over a clay ledge. Immediately downstream a riffle was formed by rubble and gravel.

The fall of the stream between the C-D and A-Z boundries (Fig. 1) has been estimated to be approximately 25 feet. This gradient imparted a current of 1.5-2.5 feet per second in the upper reaches of Section C. Below Station 2 the stream followed a narrow channel between high, sandy banks supporting a growth of aspen, birch, and balm-of-Gilead. The bottom throughout this area was mainly fine and medium gravel.

Deflectors have been established for stream improvement along the course of the stream (Shetter, Clark, and Hazzard 1949). They were constructed of logs and rough lumber and secured into the bank and stream bottom by piling. Behind these stream improvement devices the bottom differed considerably, being formed of silt and detritus. This change was especially evident where the stream flowed through the marsh and cedar swamp.

The portion of the stream designated as Sec-

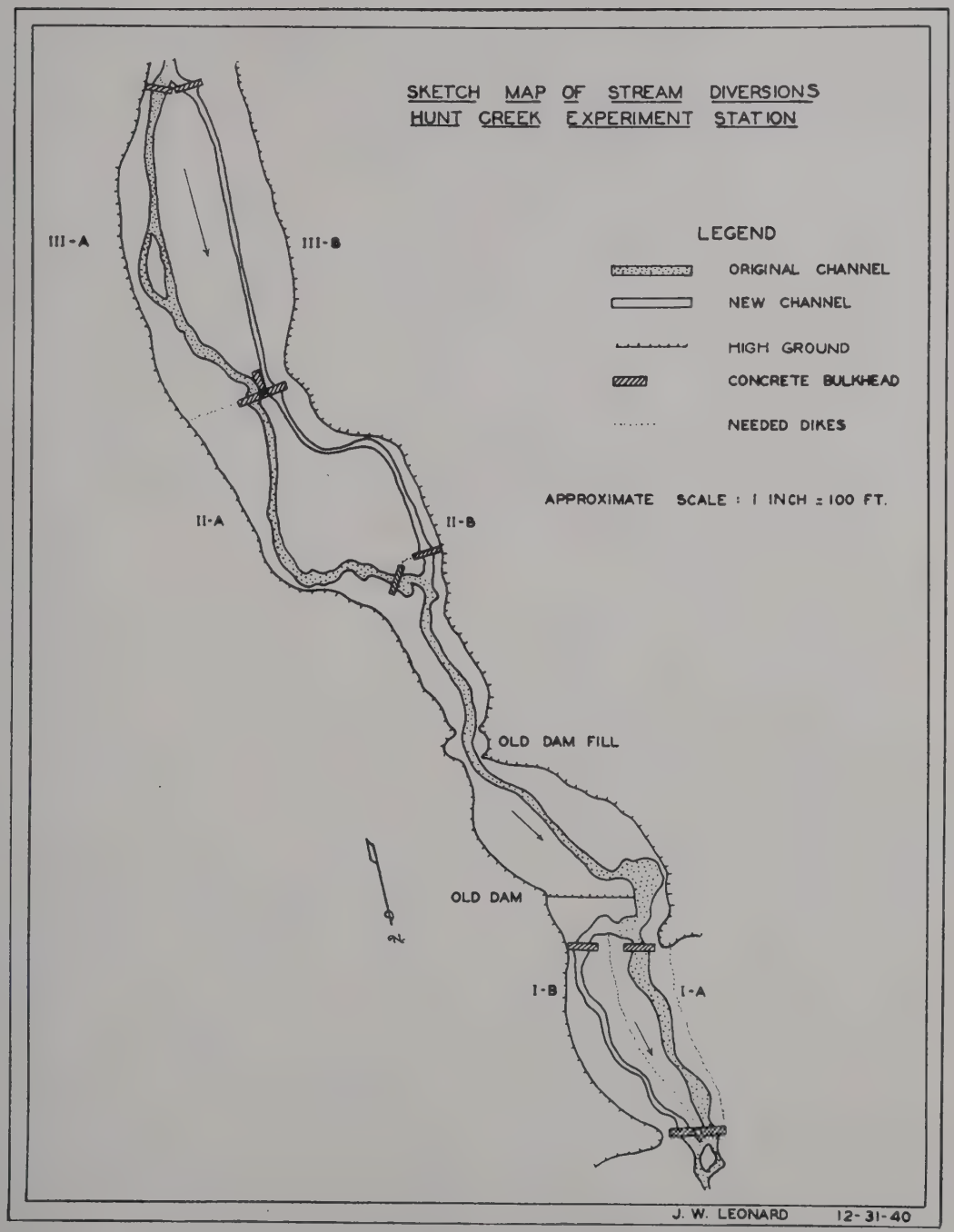

FIG. 2. Map of stream diversions, Hunt Creek Experiment Station.

tion C for trout research purposes included highlands, a series of diversions, and a portion of a cedar swamp. The diversions were located in the highlands and consisted of a series of parallel channels, or diversions from the main stream. The channels, whose flow was controlled by concrete bulkheads, were used by the station staff for experimental work on the stream fauna. The dug channels were numbered I-B, II-B, III-B, the original stream channel I-A, II-A, and III-A (Fig. 2). The lower end of Section C was cedar-tamarack swamp.

Station 3 was established near a bulkhead controlling the flow of water from diversions III-A and B. Diversion III-A had standing water about one foot deep with a bottom of muck and detritus. The stream in diversion III-B was swift and had a bottom of sand and gravel.

Station 4 was located downstream in a deep pool at the foot of a bulkhead at the head end of diversion I-B. The water was about four feet deep in the deepest portion of the pool. The bottom consisted of muck and some detritus. There was a slight current through this channel. Station 5 was located in diversion I-A about 25 feet distant from Station 4. The stream in diversion I-A was swift and had a bottom of gravel and rubble. The water was quite shallow at this station ranging from one to four inches in depth.

Station 6 established in the downstream portion of Section C, was the only station located in the cedar swamp. The stream in the swamp was slightly wider than in the highlands, and had a bottom of sand and gravel which was not typical of a cedar swamp association. The station was located downstream from a natural log jam in a pool four feet deep. Much detritus, muck, and sand had been deposited along the bank edge of the pool.

After flowing through the cedar swamp (Section B, in part, Fig. 1) the stream entered a sedge-meadow of about 10 acres in extent. This area was designated as Sections A and Z. The stream widened to 10-15 feet through this meadow as compared to 3-5 feet in the highlands. However, the stream continued to maintain a rather swift current. The bottom in this area was composed of sand with occasional patches of gravel. Deposits of muck and detritus were found in sheltered areas behind man-made deflectors and eroded portions of the bank.

Station 7 was located behind a deflector in the upstream portion of Section Z (Fig. 1) where the stream had widened to about 15 feet. Behind the deflector the bottom was composed of muck and detritus. In midstream the bottom was composed chiefly of sand with small patches of gravel exposed. Station 8 differed from the preceding stations in that the stream was much wider, being approximately 35 feet in the widest spot, and extended across a gravel bar from a washout in the east bank. The west bank had been stabilized for a short distance from the weir by reinforcing it with stone. This station was located in the lower portion of Section Z downstream from the controlling bulkhead.

Additional collections were made at Fuller Creek Pond and East Fish Lake each within the area previously described (Fig. 1). Fuller Creek Pond has an area of approximately 30 acres and has been formed by establishing a dam over an old beaver workings. Collections were made from extensive mats of *Chara sp.* growing in water about 6 feet deep close to the dam.

East Fish Lake has an area of approximately 50 acres. The lake had previously been smaller, but its area was increased by establishing a weir at the outlet (Fig. 1). Collections were made within the profundal region of the lake and were distributed along a NE-SW transect across the lake and in the outlet directly below the controlling weir.

Technique

Collections were made at biweekly intervals during the summer at permanent collecting sites. During the same period general collections were made in all sections along the stream. Samples from the permanent stations were taken from representative bottom types across the stream. Two samples were taken from each of the soft bottom muds with a dip net having a cloth of 20-25 meshes per inch. The material was then sorted through a screen of similar mesh size. The insect larvae, sand, and detritus obtained from stones in the swifter portion of the stream were preserved in the field. Collections from the bottom muds were sorted in the laboratory. All material was preserved in 10% formalin and glycerine.

To aid in the identification of the larvae, immature stages of the midges were isolated from the samples taken in the field and sorted to species as nearly as possible. The larvae or pupae were then placed in rearing jars containing moist filter paper and covered with lids. The emerging adults were allowed to mature for a period of 24 hours after emergence. They were then killed and placed in individual vials. Other culture jars were maintained in aerated one-gallon containers supplied with water and bottom mud. The emerging adults were collected in a glass jar supported by a wire screen over the mouth of the rearing container.

TABLE I. *Occurrence of Tendipedidae in Hunt Creek, Montmorency County, Michigan. A = Adults not yet associated with immature stages; A# = Adults taken at light; X = species from which larvae and adults have been associated; X' = species collected in larval, pupal and adult stages. Numbers in brackets show number of adults reared from larval samples. Classification based on Johannsen et al. (1952), and Johannsen 1937a, b.*

Character of terrain adjacent to stream	Highlands		Cedar Swamp		Marsh-Meadow		Beaver Ponds	Bottom Type
Type of stream situation	Lotic	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic	
Anatopynia decolorata (Malloch)	A(1)	..	..	..	..	..	..	Sand, detritus, and muck
Anatopynia hirtipennis (Loew)	A(4) X'	A(1)	..	..	..	..	A(4)	Lentic, stones; lotic, sand, detritus, muck
Anatopynia sp. (new species?)	..	..	..	..	X	..	..	Sand, muck
Anatopynia sp. (near plumipes)	..	..	..	..	..	..	X	Muck, detritus
Anatopynia species	X	..	X	..	X	..	X	Sand, muck, detritus
Procladius culiciformis (Linné)	A(1)	..	..	..	..	..	A(2) X'	Muck, detritus
Procladius sp. (near culiciformis)	X	..	..	..	X	..	..	
Procladius species	X	..	X	..	X	..	X	Sand, muck, detritus
Prodiamesa olivacea (Meigen)	A(1) X'	..	X	..	X	..	..	Sand, muck, detritus
Prodiamesa bathyphila (Kieffer)	A(1)	..	..	..	..	..	..	Muck
Prodiamesa species (new species?)	..	..	..	..	X	..	..	
Syndiamesa species	A(1)	..	..	..	..	..	..	Sand, muck, detritus
Psilodiamesa fulva Johannsen	..	..	X	..	..	..	..	Sand, muck, dteritus
Psilodiamesa fulva Johannsen?	..	..	..	..	X	..	..	
Metriocnemus lundbecki Johannsen	..	X	..	..	..	..	..	Sand cases on rocks
Metriocnemus species (near lundbecki)	..	..	..	..	..	X	..	Sand cases on rocks
Cardiocladius species	..	X	..	..	..	X	..	Silt and sand masses on stones
Hydrobaenus species	..	..	..	..	..	..	X	Muck and detritus
Calopsectra brunnipes Zetterstedt	..	..	X?	..	X	..	A(2) X	Muck, sand, detritus
Calopsectra dives (Johannsen)?	X	..	X	..	..	..	..	Muck, sand, detritus
Calopsectra (Micropsectra) species	X	..	X	..	..	..	X	Muck, sand, detritus
Calopsectra mutica (Johannsen)?	..	..	..	..	A*	..	..	Muck, marl, detritus
Calopsectra tenuis (Meigen)	A(1)	..	..	..	..	..	A(6)	Muck, marl, sand, detritus
Calopsectra exigua (Johannsen)	..	X	..	..	..	..	..	Cases attached to stones near clay ledges
Calopsectra exigua (Johannsen) var. b	..	X	..	..	..	..	..	Cases attached to stones near clay ledges
Calopsectra species roseiventris (Kieffer)?	..	..	X	..	X	..	..	Muck, sand, detritus
Calopsectra sp. [atridorsum (Walker) or mancus (Walker)]	..	..	X	..	..	..	..	Muck, sand, detritus
Calopsectra species	X	X	..	..	X	..	X	On stones in current and muck, sand, detritus
Microtendipes pedellus var. aberrans (Johannsen)?	..	..	..	..	..	..	X	Muck, sand, detritus
Paratendipes albimanus (Meigen)	A(7) X'	..	..	..	..	..	A(8) X'	Muck, sand, detritus
Tanytarsus species near jucundus (Walker)	X	..	..	..	..	..	..	Muck, sand, detritus
Tanytarsus (Stictochironomus) species	..	..	..	..	X	..	X	Muck, sand, detritus
Tanytarsus species	X	..	..	..	..	..	X	Muck, sand, detritus
Cryptochironomus digitatus (Malloch)	..	..	X	..	X	..	..	Muck, sand, detritus
Cryptochironomus psittacinus (Meigen)	..	..	..	..	..	..	X	Pulpy peat
Cryptochironomus species	X	..	..	..	X	..	..	Muck, sand, detritus
Tendipes tuxis (Curran)	X	..	..	..	A(1)	..	..	Muck, marl, some sand and detritus
Tendipes riparius (Meigen)	A(1)	..	..	..	..	..	..	Muck, sand, detritus
Tendipes plumosus (Linné)?	..	..	..	..	X	..	..	Muck, detritus

NOTES ON SPECIES RECORDED (TABLE I)

SUBFAMILY PELOPIINAE (= TANYPODINAE)

Pentaneura annulata (Say)

A single larva was found in Fuller Creek Pond, in a bottom of muck and marl supporting a good growth of *Chara sp.*

Anatopynia decolorata (Malloch)

One adult was reared from a larva collected in highlands from a lotic situation with a bottom composed of sand, detritus, and a variable amount of muck.

Anatopynia hirtipennis (Loew)

Ten adults were reared. These larvae occurred in all sections of the stream except the marsh area, in both lotic and lentic situations over sand, detritus, and muck botton; in current larvae were found in sand masses on stones.

Anatopynia sp. near *plumipes* (Fries)

Larvae were collected in a beaver pond whose bottom was composed of muck and detritus.

Anatopynia sp.

Larvae of this genus were distributed in each of the ecological areas bordering the stream. The genus appears to prefer a lotic situation over a bottom of sand, muck, and detritus.

Anatopynia sp. new species?

Two larvae were collected in a lotic situation in the marsh area. The bottom was composed of sand and detritus.

Procladius culiciformis (Linné)

Three adults were reared from larvae collected in lotic conditions in the highlands and beaver ponds. The bottom in each case was composed of muck and detritus.

Procladius choreus Meigen

Two larvae were collected from East Fish Lake in 9½-11 meters of water. The bottom was composed of fine marl.

Procladius sp.

The genus was represented in all associations except Fuller Creek Pond. The larvae occurred in both lotic and lentic conditions over bottoms having variable amounts of sand, muck, and detritus.

Subfamily Diamesinae

Prodiamesa olivacea (Meigen)

This constituted a major species along the stream and occurred in lotic and, to a limited extent, in lentic conditions. The bottom deposits were composed of sand, muck, and variable amounts of detritus.

Prodiamesa bathyphila (Kieffer)

One adult was reared from a larva collected in a lotic situation in the highlands. The bottom deposit was composed of sand, muck, and detritus.

Prodiamesa sp. (new species?)

A larva collected from a lotic situation in the marsh-meadow area. The bottom deposit was composed of sand, muck, and detritus.

Syndiamesa sp.

Adult collected by light in Section Z. Another adult reared from larvae collected in lotic situation in highlands. The bottom deposit was composed of sand, muck, and detritus.

Psilodiamesa fulva Johannsen

Larvae were collected in the marsh and cedar swamp in lotic situations over bottoms composed of sand, muck, and detritus.

Psilodiamesa fulva Johannsen?

One larva collected from a muck deposit in a lotic situation in the cedar swamp.

Subfamily Hydrobaeninae

Metriocnemus lundbecki Johannsen

Larvae of this species were collected from rocks in lentic situation in highlands.

Metriocnemus sp. (near *lundbecki*)

Larvae were collected from stones in lentic situation in marsh-meadow.

Cardiocladius sp.

The larvae were found within masses of sand and silt on stones in a lentic situation in the highlands and sedge-meadow.

Hydrobaenus sp.

The larvae were collected in water 3-4 feet deep at the foot of the beaver dam in the highlands. The situation was not entirely lotic, some current being present. The bottom deposit was composed of a large quantity of detritus with some muck.

Subfamily Tendipedinae (= Chironominae)

Calopsectra (*Micropsectra*) *brunnipes* Zetterstedt

Two adults were reared from larvae collected from the lotic situation within the beaver ponds. The bottom deposit was composed of muck, sand, and detritus. Additional larvae were collected from lotic conditions within the marsh-meadow and cedar swamp. The bottom deposits in the latter ecological areas were the same as found in the beaver ponds.

Calopsectra (*Micropsectra*) *dives* (Johannsen)?

Larvae were collected from the swamp and highland areas in lotic situation over bottom deposits of sand, muck, and detritus.

Calopsectra (*Micropsectra*) *sp.*

This subgenus was found in both lentic and lotic situations in all ecological areas along Hunt Creek. However, the majority of the larvae were found in a lotic condition. The bottom deposit most often consisted of muck, sand, and detritus, but occasionally extended into gravel and stones 3-5 inches in diameter.

Calopsectra (*Calopsectra*) *mutica* (Johannsen)?

Three adults were reared from larvae collected at Fuller Creek Pond and one adult was collected by light in Section Z. The bottom deposit at Fuller Creek Pond was composed of muck, marl, and detritus. The larvae appear to live in a lotic

situation and when found with *Chara* their cases are attached to the stems of the plants.

Calopsectra (*Calopsectra*) *tenuis* (Meigen)

Eleven adults were reared from larvae collected in lotic situations in the highlands, the beaver ponds, and Fuller Creek Pond. The bottom deposits were composed of sand, muck, detritus, in addition to marl in Fuller Creek Pond.

Calopsectra (*Calopsectra*) *pusio* (Meigen)

One adult was reared from larvae collected in Fuller Creek Pond. The larvae appear to be associated with *Chara sp.* which were growing in a bottom deposit of muck, marl, and detritus.

Calopsectra (*Rheotanytarsus*) *exigua* (Johannsen)

Larvae, larval cases, and one pupa were collected in a lentic situation in the highlands where the cases were attached to one side of stones near a clay ledge.

Calopsectra (*Rheotanytarsus*) *exigua* (Johannsen) var. *b*

The larval habitat is the same as that described for *C. exigua.* Larva differs from the typical *exigua* in the manner of case construction by having 6 ribs and filaments.

Calopsectra coracina (Kieffer)

Larvae of this species were collected from East Fish Lake in water 9½-11 meters deep and having a bottom of pulpy peat.

Calopsectra sp. near *roseiventris* (Kieffer)?

The largae were collected from cedar swamp in a lotic situation over a bottom of sand, muck, and detritus.

Calopsectra sp. [*atridorsum* (Kieffer) or *mancus* (Walker)]

The larvae were collected in the cedar swamp under lotic conditions over bottoms of sand, muck, and detritus.

Calopsectra sp.

The larvae of an undetermined species were found in the highlands on stones in midstream. They had the same habitat as that described for *Cardiocladius sp.* The genus was represented in lotic conditions found behind deflectors and washouts in the sedge-meadow. The bottom deposits were composed of sand, muck, and detritus.

Microtendipes pedellus var. *aberrans* (Johannsen)?

The larvae were found at the foot of the beaver dam in a lotic situation. The bottom was composed of sand, muck, and detritus.

Paratendipes albimanus (Meigen)

Large numbers of larvae were present when found at all. Fifteen adults were reared from larvae collected in lotic situations in the highlands and beaver ponds. The water ranged from 8-12 inches to 6-8 feet deep. The bottom deposit was composed of sand, muck, and detritus. This species is easily reared in the laboratory.

Tanytarsus (*Tribelos*) *sp.* near *jucundus* (Walker)

Larvae were collected where some current was present with a bottom deposit of sand, some muck and detritus. The larvae were collected in the highland area.

Tanytarsus (*Stictochironomus*) *sp.*

Larvae were collected in a lotic situation in the sedge-meadow and beaver ponds. The bottom deposit was composed of muck, detritus and variable amounts of sand. The water varied from 6 inches to 4 feet in depth.

Tanytarus sp.

Larvae were collected from the highlands and beaver ponds in a lotic situation. The bottom was composed of sand, muck, and detritus.

Cryptochironomus digitatus (Malloch)

The larvae were collected from a lotic condition in the marsh and cedar swamp where the bottom was composed of sand, muck, and detritus.

Cryptochironomus psittacinus (Meigen)

Larvae were collected from the beaver ponds in a lotic situation over a bottom of pulpy peat.

Cryptochironomus sp.

Larvae were collected from the highlands and marsh in lotic situations over a bottom of sand, muck, and detritus.

Tendipes (*Limnochironomus*) *modestus* (Say)

One adult was reared from larvae collected in Fuller Creek Pond. The larvae appeared to be associated with dense growths of *Chara sp.* and a bottom deposit composed of muck, marl, and detritus.

Tendipes (*Limnochironomus*) *nervosus* (Staeger)?

Two adults were reared from larvae collected from Fuller Creek Pond. The habitat is the same as that described for *T. modestus.*

Tendipes (*Tendipes*) *decorus* (Johannsen)

Larvae were collected from East Fish Lake at a depth of 9½-11 meters from a bottom of muck, marl, and pulpy peat.

Tendipes (Tendipes) tuxis (Curran)

This form appears to be the most abundant of the larger midges. Six adults were reared from larvae collected in East Fish Lake, Fuller Creek Pond, and the sedge-meadow. Larvae were also collected from a lotic situation in the highlands. The bottom deposits contained sand, muck, and detritus along the stream, whereas Fuller Creek Pond and East Fish Lake had considerable marl in this mixture.

Tendipes (Tendipes) riparius (Meigen)

One adult was reared from larvae collected in a lotic situation in the highlands over a bottom of sand, muck, and detritus.

Tendipes (Tendipes) plumosus (Linné)?

Several larvae were collected from the sedge-meadow in a lotic situation over a bottom of muck and detritus.

Tendipes sp.

Larvae were collected from East Fish Lake and in lotic situation in the highlands. The water ranged in depth from 8-12 inches to 28-33 feet and the bottom deposit consisted of muck, pulpy peat, some sand, with marl in the lake.

Discussion

Several interesting observations were made regarding the habitat preference of the midges. As the samples were qualitative, no conclusions can be drawn as to quantitative occurrence of components of the midge population. Observations of the fauna illustrate that it is more readily divided into lentic and lotic habitats than into the four ecological areas, based on stream valley characteristics designated earlier in the paper. Of the 15 genera and 34 species recorded, only 3 genera and two named species were found in the lentic environment. This fauna included only *Cardiocladius sp., Calopsectra exigua, Calopsectra exigua* var. *b* and *Calopsectra sp.* The remaining species had a lotic preference.

The principal factors affecting this distribution appear to be current and bottom type. This conclusion is in agreement with results obtained by Sprules (1947) on streams in Algonquin Park, Ontario. He stated that the nature of the bottom, which is also of considerable importance in limiting the distribution of insects in a stream, is so closely related to current that it is difficult to discuss the two factors separately. With regard to the bottom deposit none of the lotic fauna were found on clean surfaces excepts *C. exigua,* or closely related forms. It will be recalled that this midge constructs a cone-shaped case having filaments at the larger end. It is attached to rocks either by a petiole at the smaller end or along one side of the case.

The *Cardiocladius sp.* larvae collected from the lentic environment differed from *Calopsectra exigua* in the manner in which the cases were constructed. The former lived in compact masses of microscopic sand grains and detritus held together by net-like filaments spun by the animal. Within the mass they moved about in tunnel-like chambers quite different from the tubes of the midge larvae inhabiting the lotic environment.

The masses were found on a heterogeneous assemblage of stones ranging in size from 2-8 inches in diameter. The larvae appeared to form their own cases upon rocks and stones located only in portions of the stream having clay bottoms with some fine detritus present. Cases were located on any portion of the exposed surface of the stone.

Frequently a few larvae of the genus *Calopsectra* were found associated with the *Cardiocladius sp.* larvae. Both inhabited the same masses of sand and detritus.

The remaining 32 species were distributed in the lotic environment extending from the sand deposits into the detritus-filled muck. The sand deposits were generally quite narrow and finger-like in the small pools and shallows behind the deflectors. The sand ridges extended out into the stream on the current side, but where suffcient current was available to move the sand a definite break in bottom type was noticed—the bottom here would be covered with gravel and small stones.

The sand deposit appeared to have a specific fauna, comprised of *Anatopynia sp., Prodiamesa olivacea,* and *Calopsectra sp.* Further collections should be made to determine the exact limitations of the species found there. *Anatopynia* sp. populated sand deposits with some silt. *P. olivacea* was found in a variety of mixtures of muck and sand, but not abundantly in the heavy deposits of muck. Larvae of the genus *Calopsectra* were found distributed in bottom deposits ranging from a mixture of sand and silt to muck areas. Perhaps one or more species will be found that require a more sandy habitat. Some tubes were constructed from sand grains adhering to a net spun by the larvae. Others were constructed of sand grains first, then particles of silt and long pieces of detritus.

The change in populations from midstream through gravel, sand, to muck and detritus has been discussed by Hall (1951). From surveys of English acid and chalk streams he reports that

it has been demonstrated that the percentage of Tendipedidae in the bottom fauna of the various types of stream beds decreases considerably in the absence of fine detritus, and also decreases with the increase in speed of current flow. This fact is well illustrated when sampling sand, sand-muck mixtures, muck, and muck-detritus habitats. The population increases rapidly as the muck-detritus habit is reached. Some species, for example P. *olivacea, Calopsectra sp., Procladius sp.,* and *Anatopynia* sp., occurred in a series of specific habitats extending from sand to muck. Other species appeared to be restricted to pure mixtures of sand and muck, or muck and detritus. Further research on the sand-muck complex will have to be done to disclose any specific requirements of individual species.

Several species of midges inhabiting muck-detritus were reared in sufficient quantities to accurately establish their presence during the survey. *P. albimanus* was restricted to backwaters having a bottom composed of muck-detritus. Areas of this nature were not common, but when they occurred the larvae were present in large numbers. These larvae constructed tubes of considerable length from the particulate matter and detritus of the bottom muck.

Larvae of *T. tuxis,* a large midge, were found in areas similar to those favored by *P. albimanus.* Large numbers of the larvae tentatively identified as this species were encountered in a shallow pool in diversion I-B. Adults of *T. tuxis* have been reared from the bottom mud of Fuller Creek Pond.

A comparison of the fauna of beaver ponds, highlands, sedge-meadow, and cedar swamp habitats cannot be made with great accuracy due to the small number of adults reared from the larvae collected. It does appear that the subfamilies Pelopiinae, Diamesinae, and Hydrobaeninae are encountered more frequently in the stream habitat than Tendipedinae. Of the above subfamilies, Pelopiinae was represented by three genera and nine species; Diamesinae by three genera and six species; Hydrobaeninae by three genera and four species; the Tendipedinae by six genera and 26 species. The genus *Calopsectra* was the most common form representing the Tendipedinae.

Of the various genera collected *Anatopynia, Procladius, Prodiamesa, Calopsectra, Cryptochironomus,* and *Tendipes* were represented in all general areas selected along the stream.

Several species were well represented in the stream with respect to the ecological associations. *A. hirtipennis* was collected from the beaver ponds, highlands, and sedge-meadow areas. *P. olivacea* was one of the most widely distributed midges along the stream, appearing in three of the four areas. *C. brunnipes,* another common midge, was found in all areas except the highlands. It is quite possible it will be found there as the larvae could be overlooked because of their small size.

The distribution of *Cryptochironomus digitatus* and *T. tuxis* appeared to be restricted. The former was represented in only two areas, including the larger bodies of water. It is possible that this species appears in other areas and that its emergence is early in the spring. Under these conditions larvae would not have been collected in larger numbers as the survey started during the latter part of June. *T. tuxis* occurred more frequently than did *C. digitatus,* but is apparently quite restricted to a specific bottom type.

The remaining genera and species were never recovered in sufficient numbers as larvae or adults to give a clear picture of their distribution.

Acknowledgments

Gratitude is expressed to Dr. David S. Shetter and the staff of the Hunt Creek Experiment Station for suggestions and criticisms of the field and laboratory work. Field and laboratory equipment was furnished by the Institute for Fisheries Research and Dr. Robert C. Ball, Department of Fisheries and Wildlife, Michigan State College. Slides and museum material for some determinations were obtained through Dr. Henry Dietrick, Department of Entomology, Cornell University. Thanks are also due Drs. Justin W. Leonard and Albert S. Hazzard for critical reading of the manuscript. Financial aid for the research was granted by the Institute for Fisheries Research, Michigan Department of Conservation.

Summary

1. A preliminary investigation of the midge fauna was made on Hunt Creek, Montmorency County, Michigan, during the summer of 1952.

2. All collections made were qualitative and based upon natural ecological areas along the stream, namely beaver ponds, highlands, cedar swamp, and sedge-meadow. Additional samples were taken from East Fish Lake and Fuller Creek Pond.

3. A total of 15 genera and 34 species was found representing the stream midge fauna.

4. The fauna did not appear to be distributed along the stream according to the natural ecological areas selected, but individiual species were restricted by current and bottom type.

5. Of the 34 species recorded, only *Cardiocladius sp., Calopsectra exigua,* and *C. exigua* var. *b* were found in the lentic habitat. The remaining

31 species were found in the lotic environment.

6. *Anatopynia sp., Prodiamesa olivacea,* and *Calopsectra sp.* appear to be restricted to a bottom containing some proportion of sand. *Paratendipes albimanus* and *Tendipes tuxis* were restricted to deposits of muck-detritus.

7. The genera *Anatopynia, Procladius, Prodiamesa, Calopsectra, Cryptochironomus,* and *Tendipes* were distributed throughout the sections of the stream investigated.

References

Hall, R. E. 1951. Comparative observations on the chironimid fauna of a chalk stream and a system of acid streams. Jour. Soc. British Ent., **3**: 253-262.

Johannsen, O. A. 1937a. Aquatic Diptera, Part III. Chironomidae: Subfamilies Tanypodinae, Diamesinae, and Orthocladinae. Cornell Univ. Agr. Exp. Sta., Mem. 205, 84 pp.

———. 1937b. Aquatic Diptera, Part IV: Chironomidae: Subfamily Chironominae. *Ibid.,* 210, 52 pp.

Johannsen, O. A., H. K. Townes, F. R. Shaw, and E. G. Fisher. 1952. Guide to the insects of Connecticut, Part VI. The Diptera or true flies. Fifth Fasicle: Midges and gnats. Conn. State Geol. and Nat. Hist. Surv., Bull. 80, 255 pp.

Leonard, J. W. 1940. The feeding habits of legal brook trout in Hunt Creek during the 1940 fishing season. Inst. Fish. Res. Rep. No. 659. [Processed.]

———. 1942a. Bottom fauna production in Section B of Hunt Creek prior to installation of improvement devices. Inst. Fish. Res. Rept. No. 788. [Processed.]

———. 1942b. Some observations on the winter feeding habits of brook trout fingerlings in relation to natural food organisms present. Trans. Am. Fish. Soc. (1941), **71**: 219-227.

Roelofs, E. W. 1944. Water soils in relation to lake productivity. Michigan State Coll., Tech. Bull. 190, 31 pp.

Shetter, D. S. and J. W. Leonard. 1943. A population study of a limited area in a Michigan trout stream, September, 1940. Trans. Am. Fish. Soc. (1942), **72**: 35-51.

Shetter, D. S., O. H. Clark and A. S. Hazzard. 1949. The effects of deflectors in a section of a Michigan trout stream. Trans. Am. Fish. Soc. (1946), **76**: 248-278.

Sprules, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Studies, Biol. No. 56., Pub. Ont. Fish. Res. Lab., No. **69**: 1-81.

PHYTOPLANKTON AND TURBIDITY IN WESTERN LAKE ERIE

JACOB VERDUIN
The Franz Theodore Stone Institute of Hydrobiology, Put-in-Bay, Ohio

Introduction

During a five-year period beginning September 1948, the phytoplankton populations of western Lake Erie have been sampled frequently over a large portion of the western basin (Verduin 1951a, 1951b). In conjunction with the phytoplankton studies, the turbidity of water samples has been studied. These data afford an opportunity to assess relationships between turbidity and phytoplankton abundance from the accumulated data of several years' sampling over an extensive area. Chandler and Weeks (1945) presented data from four years of phytoplankton sampling, mostly at a single station near Put-in-Bay. They showed that the annual crop of 1941 was 3.5 times higher than the crop of 1940, the poorest year. They did not compute average annual turbidities for comparison, but they state that "physical factors rather than chemical factors usually control vernal phytoplankton production in western Lake Erie," and they list high turbidity as a major controlling factor. It has been pointed out, however (Verduin 1951a), that samples at a single station are not representative of a large area, so the relationships between turbidity and phytoplankton crops in a water mass cannot be determined without sampling frequently over the area in question. Phytoplankton and turbidity data obtained from extensive areas in western Lake Erie are presented and discussed below. Determinations of the light-quenching effectiveness of suspended particles in waters of the Bass Islands region are also presented.

Methods

The method of phytoplankton sampling has been described previously (Verduin 1951a), and it is sufficient to say that the phytoplankton were concentrated by filtration through a No. 25 bolting cloth disk and were estimated in volumetric units. It should be pointed out that the filtration of water through such a disk is accomplished without subjecting the cloth to high pressures. The height of water over the disk is never greater than 2 cm., and this method retains many cells which are forced through such bolting cloth when a sample is obtained with a net, hauled in the usual fashion. For example, a form of *Cyclotella* having a diameter of 12 μ, occurring in chains about 50 μ long, has at times constituted about half of the phytoplankton volume in the community retained by the disk.

But analysis of net hauls showed that about 80% of the *Cyclotella* retained by the disk was absent from the net samples.

During 1949 and 1950, turbidities were determined by measuring light transmission by water samples in a Beckman spectrophotometer ($\lambda 720$) and relating these values to a standard curve obtained with a suspension of diatomaceous earth. After 1951, light penetration was measured at each sampling place with a submarine photometer (Weston photronic cell). The data were plotted on semi-log graphs and the depth at which 1% of surface light intensity occurred was determined. The relationship between the spectrophotometer determinations and the photometer measurements has also been determined (Verduin 1952) so the 1949-50 data have been converted to the same units as are obtained with the submarine photometer. All turbidity data, therefore, are shown as "depths associated with 1% of surface light."

Phytoplankton samples concentrated with a No. 25 bolting cloth net have been used to determine the ratio of ash-free dry weight to phytoplankton volume. A 100 ml. sample of known phytoplankton content was filtered through a bolting cloth disk. The phytoplankton was removed from the disk by inserting it in a 50 ml. erlenmeyer flask, and resuspending the phytoplankton in two washes of distilled water. The suspension was transferred to a crucible and oven-dried. Weights were obtained with a Chainomatic balance, and ignition in porcelain crucibles was carried out over a carbon-free gas flame.

The dry weight of suspended particles, used in estimating the effectiveness of light-quenching (k in Beer's Law) by suspended particles in waters of the Bass Islands region, was determined by D. C. Chandler using the method described by him (1942). Those data were obtained in a cooperative sampling program carried out by D. C. Chandler, A. S. Bradshaw, and Verduin during 1948-49.

Results and Discussion

Turbidities and phytoplankton crops of 1949-1953

In Table I, the average depths associated with 1% of surface light intensity during specified periods are presented. These values are averages of several sampling trips and represent 12-20 samples per trip. They can be regarded as a reliable estimate of average conditions in a large part of the western basin. The highest phytoplankton crop observed during each period is also shown. Each of these values is an average of all samples taken on the day when the peak crop was observed. The crop observed in April, 1949, was the largest crop observed during the 5-year period. An area comprising about two-thirds of the western basin had an average standing crop of 16 mm^3 per liter. The highest crop of 1950 was only one-fifth as high.[1] It may be that high turbidities were a major factor in retarding phytoplankton growth during the spring of 1950. That year showed the highest average turbidity of the five-year period. But during the springs of 1951-52-53, the maximal crops were even lower than in 1950, although light penetration was more favorable than during 1949. So it is obvious that the low crops of 1951-52-53 were not limited by high turbidities. An analysis of solar radiation curves (from the continuous-recording pyrheliometer maintained at the Institute) for the 1951-52-53 seasons showed that this factor was no less abundant than in 1950, but was slightly below the curve for 1949 (Verduin 1951b).

Table I. *Average depths associated with 1% of surface light, and the maximal phytoplankton crops observed during springs of 1949-1953*

Spring of:	1949	1950	1951	1952	1953
Average depth associated with 1% of surface light (meters)...	4.8	3.5	6.6	5.4	7.2
Maximal standing crop ($mm.^3/l.$) Average of all samples taken from western basin on date of peak population.....	16	3	1	2	1

The pattern of turbidity in the western basin

When light penetration data for different portions of the western basin are examined a significant pattern emerges. In Figure 1, the average depth associated with 1% of surface light is shown for different positions in the areas which were studied most intensively during the springs of 1950 and 1951. This figure shows that the entire water mass in the eastern half of the western basin showed low light penetration during the spring of 1950, but the highest turbidities were observed in the region of the Bass Islands, with decreasing turbidities to the northward and eastward. In 1951, the waters were much clearer than in 1950, but the same relative pattern is evident; the highest turbidities were observed in the Bass Islands region, with clearer waters to the northwest, north, and eastward. Another feature of the 1951 map is significant: the waters northwest of the

[1] In a recent paper (Verduin 1952) the crop of 1950 as portrayed in Figures 1 and 2 is too high. The exponents in the legends of those figures should be —9 and —8 respectively, instead of —10, and —9.

Bass Islands were clearer than the waters to the northeast. Similar maps have been constructed for the springs of 1952 and 1953, and for the fall seasons of 1951 and 1952. These maps are not reproduced here, but they confirm the pattern apparent in the 1951 map. They show that the highest turbidities were found in the Bass Islands region, with decreasing turbidities to the northeastward and northwestward, but the waters northwest of the Bass Islands were consistently clearer than those to the northeast.

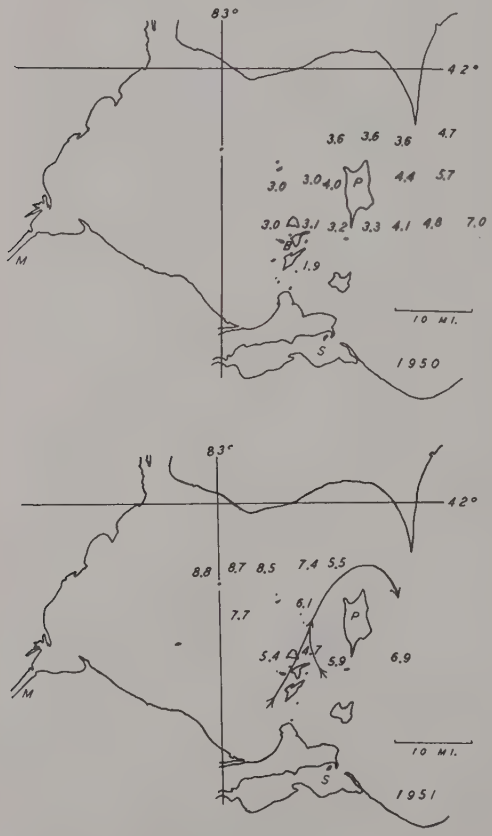

FIG. 1. Average depths (meters) associated with 1% of surface light intensity in different parts of western Lake Erie during the springs of 1950 and 1951. P identifies Pelee Island, B, the Bass Islands, S, Sandusky Bay, M, Maumee River. The arrows indicate path of water flow caused by rotational movement around Pelee Island.

This pattern of turbidity becomes comprehensible when the currents of western Lake Erie are considered. The author has referred to the current gyre around Pelee Island in a previous paper (1951b). Verber (1953) has measured the average net flow through the channels north of Pelee Island and compared it with the flow through the channels south of Pelee Island. His data show that the outflow through the channel north of Pelee Island exceeds the combined inflow of the tributaries pouring into the western basin, and that there is a net inflow of water to the western basin through the channels south of Pelee Island. The gyre, therefore, appears to be more pronounced than previous workers realized, and it prevents eastward movement of waters from the region of the Bass Islands. These waters contain the turbidity injected by the south shore tributaries of the western basin, including contributions from the Sandusky River, which are deflected into the island region by the gyre's rotation. The turbid waters move northward, leaving the western basin via the passage northeast of Pelee Island. They are subject to dilution enroute by the clearer northern waters, but the resultant water masses are consistently more turbid than the waters northwest of the Bass Islands.

Relation of turbidity to phytoplankton crops

During the spring of 1950 a phytoplankton community, confined to a small area around Pelee Island, was sampled, and a different community in the clearer waters about twenty miles east of Pelee Island was studied simultaneously (Verduin 1952). Because waters of widely different turbidities were sampled during that season the data can be used to portray the relationship between turbidity and phytoplankton crops in western Lake Erie. In Figure 2, the observed phytoplankton crops are graphed against the depth associated with 1% of surface light at each sampling position. These points are values obtained from individual samples; they are not averages of several samples. The position of the 1949 crop on such a graph is indicated for comparison.

The large scatter between abscissa values of 3 and 6 results from the fact that samples in early spring, before the phytoplankton pulse developed, were uniformly low regardless of turbidity. As the season progressed, the phytoplankton crops increased most rapidly in the waters of intermediate turbidity. The crops remained low in the most turbid waters and showed only slow rates of increase in the clearest waters. A line has been drawn through the left hand boundary of the scatter diagram, including the 1949 statistic. It seems likely that light supplies exercised a major limiting influence on the size of standing crops lying on this line. The crops indicated by points lying to the right of this line must have been influenced importantly by factors other than light supply. The line takes on added significance when the total depth of the water mass is considered. In most

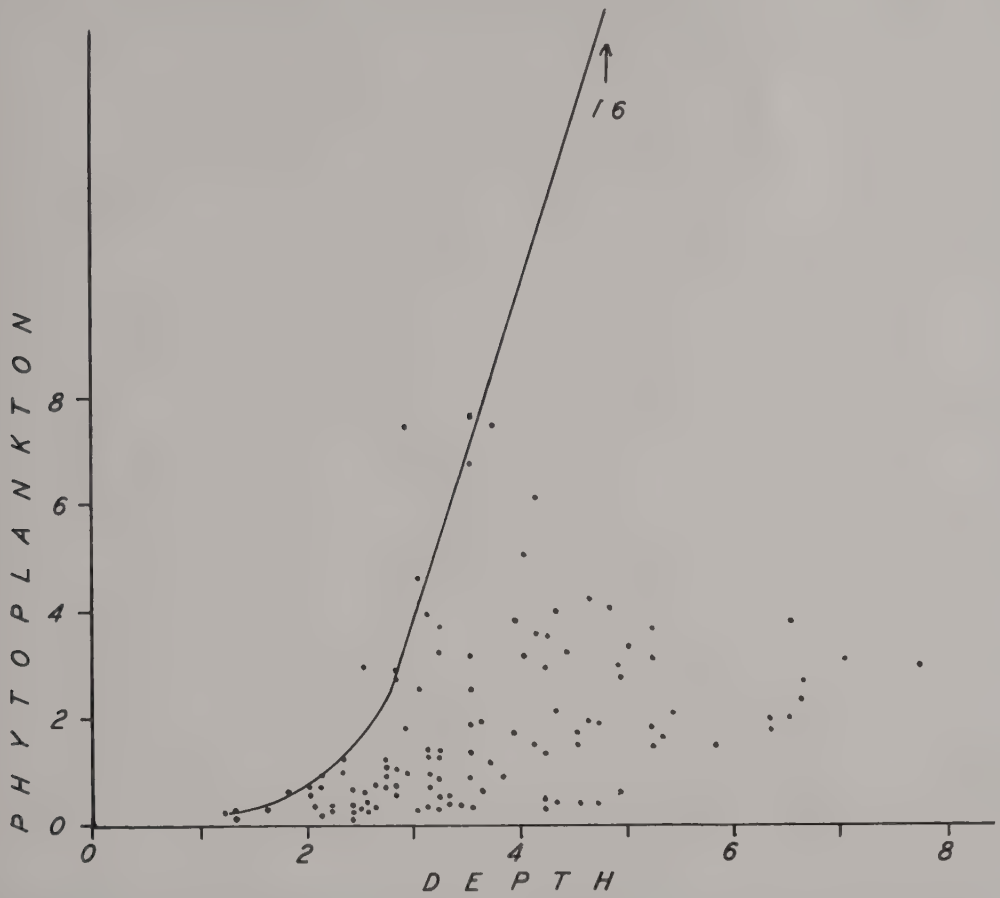

FIG. 2. Standing crops of phytoplankton (mm.³/1.) graphed against depth (meters) associated with 1% of surface light intensity; data obtained during spring of 1950. The maximal crop of 1949 is indicated by arrow, top of graph.

of the area sampled this depth is about 10 m., and turbulence insures uniform dispersal of phytoplankton in the vertical direction. Thus, even the abundant phytoplankton crop of 1949 developed under conditions such that half of the water column was essentially in darkness. The average time per day spent in the lighted zone by a phytoplankter must have been about 6 hours. It is reasonable to assume that such conditions represent severe light limitation. It should be emphasized, however, that several factors can be limiting simultaneously (Verduin 1953) and that light supplies are somewhat less than abundant even in the region to the right of the line in Figure 2.

The data appearing in Table I raise an interesting question: if crops so large as the one observed in 1949 can be produced in western Lake Erie, why did the clear waters of the 1951-52-53 seasons not support similar crops? A tentative explanation can be offered, drawing on the knowledge of current patterns in the western basin. During periods of prolonged, powerful northeast winds the Pelee Island gyre expands, and waters pour into the western basin from the northeast through channels south of Pelee Island. These waters cut across the more turbid waters in the Bass Islands region mixing with them and creating a large water mass of intermediate turbidity in the western basin. Conclusive evidence of such a process was first published by Andrews (1948), and a similar effect was detected in 1949 (Verduin 1951a). Curl[2] has shown that the soluble phos-

[2] Curl, H. C. 1951. The distribution of phosphorus in western Lake Erie and its utilization by natural phytoplankton populations. M.S. Thesis. The Ohio State University.

phorus content of turbid waters in the Bass Islands region may be as high as 40 μg./1. during the spring season and that Maumee River waters may have phosphorus content as high as 140 μg./1. The clear waters northwest and east of the Bass Islands, however, showed an average phosphorus content of less than 3 μg./1. during the spring of 1951, and values as low as 0.1 were observed. So it is reasonable to assume that the waters of intermediate turbidity created during mixing by the expanded gyre are more fertile than clearer waters which have not been subjected to such a process. During the springs of 1950-51-52-53, no pronounced expansion of the gyre, with attendant clearing of waters in the southern part of the basin, was detected. It may be that phytoplankton crops of the magnitude observed in 1949 arise only during springs when an expanded gyre, opportunely timed, powered by northeast winds of appropriate strength, direction and duration, dilutes fertile turbid waters creating a large water mass in the western basin having enhanced fertility plus sufficient transparency to favor utilization of the fertilizer by phytoplankton.

The significance of non-linear log-light vs. depth graphs

In a previous paper (Verduin 1951a) it was shown that non-linear plots of the logarithm of light intensity vs. depth frequently are obtained in western Lake Erie. A typical plot showing this phenomenon is presented in Figure 3. Usually a sharp break occurs between two sets of points and a straight line can be drawn through each set of points, indicating that two water masses having different turbidities lie, one above the other, and that turbidity within each water mass is practically uniform with depth. Sometimes more than two layers are indicated, and plots have been obtained with four distinct slope-changes.

The most reasonable explanation for such data is that water masses of differing turbidity have converged, resulting in formation of such layers. It is significant that the lower layer is usually the more turbid, and would consequently have the higher specific gravity. Stratification of this kind must be a transient thing in western Lake Erie, because temperature, plankton, and chemical characteristics show a high degree of uniformity with depth (Chandler 1940) and the dissimilar water masses so layered are likely to be homogenized within a matter of hours, or at most days, by the turbulence created by seiche-powered currents. But, although transient, the phenomenon is a continuously recurring one, wherever water masses of differing turbidity converge. Therefore a study of the frequency of occurrence of this phenomenon in different parts of the western basin will show where the principal regions of such convergence lie.

To study the relative frequency of such stratification in western Lake Erie, all the log-light vs. depth plots obtained during 1951 and 1952 were used. From these data ratios of broken-line plots to straight-line plots were computed for different parts of the basin. These ratios are entered in the map of Figure 4. When the ratio is less than 1 it indicates that turbidity was uniform with depth in the majority of samples in that region. When the ratio is greater than 1 it indicates that stratification was detected more often than not. The highest ratios should indicate the regions of most frequent convergence of water masses having different turbidities. These regions lie west and north of the Bass Islands. The waters in the Bass Islands region, eastward, and northeastward were usually uniform from top to bottom. The waters west and north of the Bass Islands showed a layer of relatively clear water lying above a layer of more turbid water one-half to two-thirds of the time.

These observations are consistent with the current pattern described above. The waters within the Pelee Island gyre have fairly uniform properties in the vertical direction. Turbid waters are fed into the gyre in the region of the Bass Islands, and as they move northeastward they come in close contact with clearer waters to the west and north; thus frequent creation of strata results. It may be that the regions of highest ratios mark the average position of the western boundary of the gyre. As has been emphasized above, the maximal westward boundary of the gyre, when expanded by northeast winds must lie farther inside the western basin.

The effectiveness of light-quenching by suspended particles in western Lake Erie

The Lambert-Beer's Law,

$$\frac{I}{I_o} = e^{-kdc} \qquad (1)$$

relating concentration (c) of light-quenching material, and thickness (d) of the column in which light is quenched, to the ratio of observed light (I) to incident light (I_o) can be used to evaluate the extinction coefficient (k) of suspended particles in natural waters. Light measurements with a submarine photometer provide experimental values of I_o at the surface, and of I at various depths. The value of c can be estimated by centrifugal separation of suspended particles and determination of the dry weight contained per unit volume of water.

The k in the above expression should not be confused with the extinction coefficients computed

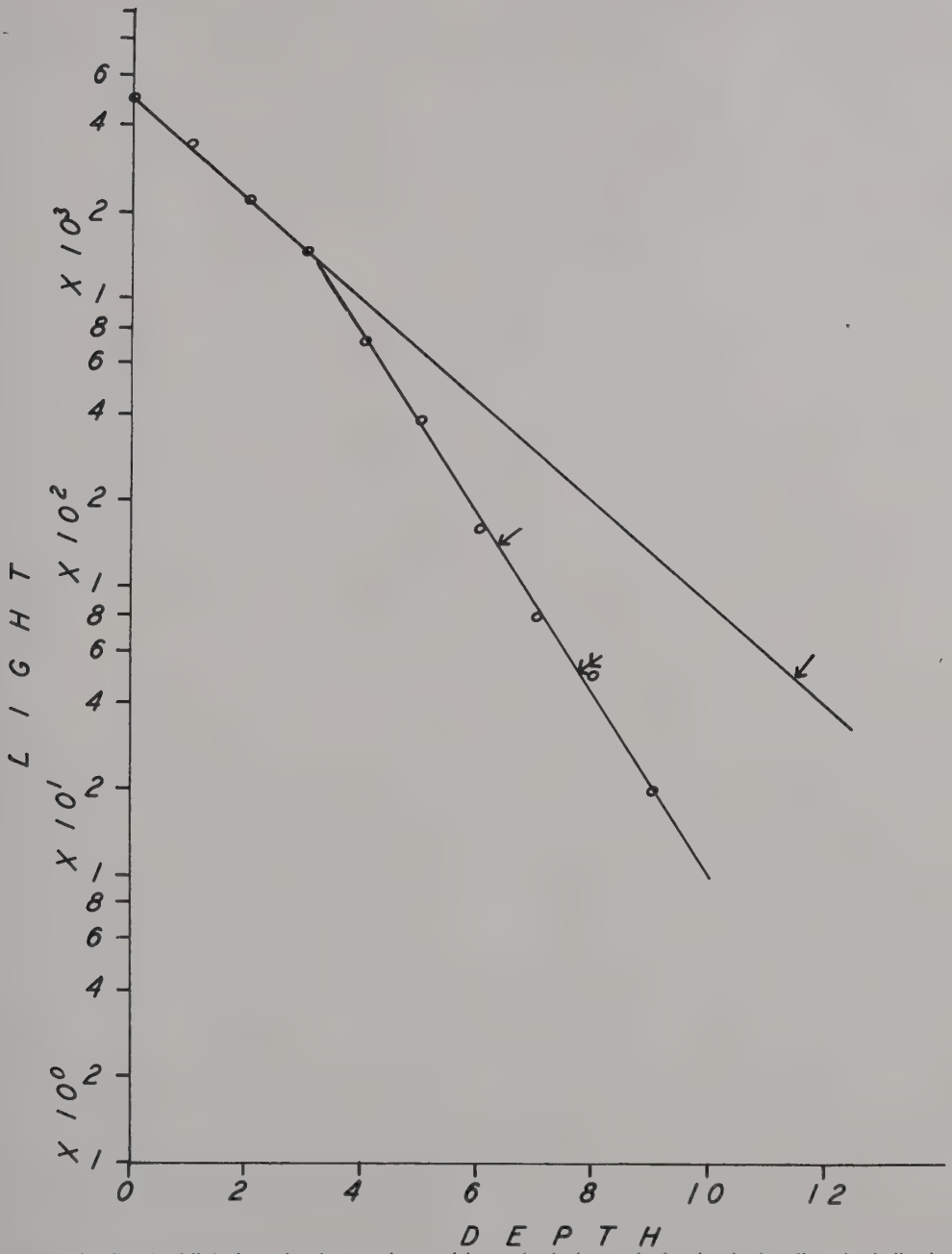

FIG. 3. Graph of light intensity (μamps, log. scale) vs. depth (meters) showing broken-line plot indicating strata of differing turbidity. The single arrows indicate depth associated with 1% of surface light for each stratum, the double arrow indicates depth associated with 1% of surface light in the total water column.

by Clarke (1939) or Whitney (1938), who used Lambert's Law:

$$\frac{I}{I_o} = e^{-kL},$$

where L is the depth at which I was observed. This k contains the variable c in Beer's Law and provides no more information than the transmission per meter, or the depth associated with a

FIG. 4. Ratios of broken-line to straight-line log-light vs. depth plots in different portions of western Lake Erie. Ratios were computed from all data obtained in 1951 and 1952. The highest ratios probably indicate the average western boundary of the water mass which rotates around Pelee Island (P).

specified fraction of surface light, provides. But when the quantity of suspended matter is determined, the k value computed from the Lambert-Beer's Law provides an index of the light-quenching effectiveness of suspended matter.

During the fall of 1948, and most of 1949, light penetration and the dry weight of suspended matter were determined at approximately two-week intervals for two stations near Put-in-Bay. The data provide an opportunity to compute the k value for suspended particles in waters of the Bass Islands region. Computation is facilitated if the Law is written as follows:

$$\text{Log}_e \frac{I_o}{I} = kdc \qquad (2)$$

from which it follows that

$$k = \frac{\text{Log}_e \frac{I_o}{I}}{dc} \qquad (3)$$

If we set I_o/I equal to 100, *i.e.* observed light is 1% of surface light, and set d equal to d', the depth associated with 1% of surface light, then k can be evaluated using the equation:

$$k = \frac{4.6}{d'c} \qquad (4)$$

For example, the highest c value observed during the period of study was 35.9 mg./1. It was associated with a d' value of 1.2 m., so the k value equals 0.107. The highest d' value observed was 7.6 m., and was associated with a c value of 5.4, yielding a k of 0.112.

Figure 5 is a bar graph showing the frequency distribution of k values in 35 samples taken during 1948-49. Only samples associated with straight-line log-light vs. depth plots were used in this survey. Uncertainties attributable to experimental error are not greater than ± 0.01. Of these samples 27 showed k values between 0.11 and 0.15. The values above 0.19 represent 2 samples taken on November 24, 1948, at stations about 3 mi. apart. The d' values at both stations were 2.3 m., the c values were 10.1 and 10.0 mg./1., yielding k values of 0.198 and 0.200. In these computations the extinction caused by the water

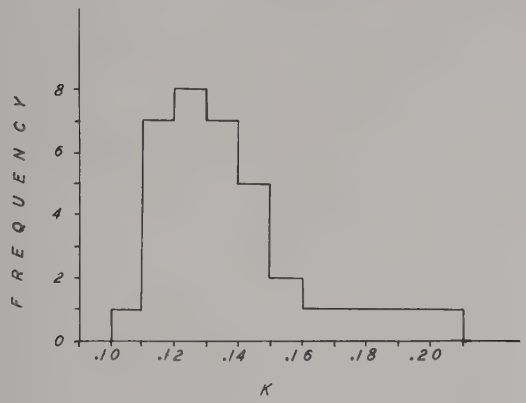

FIG. 5. Frequency distribution graph of extinction coefficients (k) from 35 samples obtained in the Bass Islands region.

itself has been neglected, because it represented only a few per cent of the observed extinction. In clearer water it becomes increasingly important. Whitney (1938) shows that the extinction coefficient for distilled water has a value of 0.03, so a correction can be made by using the equation:

$$k = \frac{\frac{4.6}{d'} - 0.03}{c} \qquad (5)$$

In the above computations light readings were not corrected for zenith sun (Whitney 1938). Log-light vs. depth plots, even on bright days, showed no significant differences in slope that could be correlated with sun angle. It seems likely that the scattering by suspensoids is so great that light, below a few decimeters, is as diffuse as light on a cloudy day. Neither has the mean path length of 118 cm./m., determined by Whitney (1938) for diffuse light, been applied above, because it would only serve to reduce each k value by a constant factor of 1.18.

Data obtained in a private communication from Dr. F. F. Hooper (Inst. for Fisheries Research, Ann Arbor, Mich.) for West Lost Lake, Mich. contained three sets of data from which k could be computed. The values obtained were 0.109, 0.123, and 0.101. Depths associated with 1% of surface light were as high as 15 m. Data obtained in a private communication from Dr. Richard T. Hartman (University of Pittsburgh) for Sanctuary Lake (Pymatuning Reservoir) provided five sets of data from which k could be computed. The values were: 0.148, 0.172, 0.159, 0.181, 0.188. Depths associated with 1% of surface light were as small as 0.4 m. The values for West Lost Lake and for Sanctuary Lake all lie within the range appearing in Figure 5. But the values for West Lost Lake all lie below the mean for western Lake Erie, and those for Sanctuary Lake all lie above it, indicating that the average effectiveness of light-quenching by suspensoids of West Lost Lake was 20% lower, and of Sanctuary Lake 30% higher, than the average for waters of the Bass Islands region.

Figure 5 shows that the range of k values is small considering the wide range of c and d' values encountered, indicating that the effectiveness of light-quenching by suspended particles in waters of the Bass Islands region was surprisingly uniform. But though the range of k values was small, statistically significant differences can be demonstrated from time to time and place to place. A wider application of this method should yield valuable information regarding the light-quenching effectiveness of different kinds of suspended particles. The extensive survey of Wisconsin lakes made by Whitney (1938) would have provided such information if he had determined the concentration of suspended particles instead of allowing this variable to exercise major control over the values of his extinction coefficient.

Studies of this type have not yet been extended to the clearer waters northwest and east of Put-in-Bay. Neither has a correlation of average particle size with k value been attempted. Dissolved pigments have not been observed in the waters of western Lake Erie. Waters emerging from the centrifuge, when tested in the spectrophotometer, show about the same transmittance as distilled water, indicating that differences in light-quenching are attributable to suspended particles. In waters containing dissolved pigments, an important part of light-quenching may be attributable to their influence, and a computation of k value based only on the depth associated with 1% of surface light and the concentration of suspended matter would be misleading.

The relatively small variation observed in the extinction coefficient values of Figure 5 makes it possible to estimate, approximately, the load of suspended particles in a water mass whose transparency is known. For example, the clear waters observed northwest of the Bass Islands in 1951 showed 1% of surface light penetrating to 8.8 m. The average load of suspended particles (using a k value of 0.13) must have been about

$$\left(\frac{4.6}{8.8 \times 0.13}\right)$$

4 mg./1. If this is regarded as fairly representative of the water entering the western basin through the Detroit River, then the additional load of suspended particles acquired in the western basin during the turbid spring of 1950 can be

computed. The average depth associated with 1% of surface light during the spring of 1950 was 3.5 m., representing a load of suspended matter equal to 10 mg./1. If the difference of 6 mg./1. can be assumed to represent additions acquired in the western basin, then the tons of suspended matter acquired can be computed from a knowledge of the volume of water contained in the portion of the basin that was sampled. The area covered in 1950 comprised about half of the western basin, and represented about 12 cubic km. of water. An addition of 6 mg./1. would correspond to 7×10^4 metric tons of suspended matter in this region. It is interesting to compare this figure with the silt injection by the Maumee River, which is the major source of silt contributions to western Lake Erie. Mr. C. V. Youngquist (Chief of the Division of Water, The Ohio Department of Natural Resources) has kindly provided data showing the tons of silt carried by the Maumee River from April 12 to May 12, 1950. Those data show that a total of 26×10^4 tons of silt was injected by the Maumee during the period; a total of 23×10^4 metric tons. This entire silt load would not remain in suspension after entering the quieter waters of the lake, but data of Lamar (1953) show that 49% of the silt load in Maumee River water has a particle size of less than 2 μ. It is not unreasonable to assume that a similar fraction of the Maumee silt load is retained in suspension by the turbulence of western Lake Erie waters. Such a fraction of the silt injected by the Maumee during the month preceding May 12, 1950, would amount to 11×10^4 metric tons, a figure having the same order of magnitude as the 7×10^4 metric tons computed above as the addition acquired in the western basin. The rate of flow through western Lake Erie is such that the total water volume is displaced in an average period of two months, so it is realistic to compare one month's silt injection with the acquired load in one-half of the western basin. The above computations suggest that the major part of the turbidity acquired in the western basin in a turbid year such as 1950, can be attributed to injection by the south shore tributaries.

The magnitude of maximal phytoplankton crops

Many investigators of phytoplankton abundance have been, and are, content to report crops in terms of number of cells per liter, although it is obvious on casual inspection of a community that the large forms have cell volumes many times greater than the small forms. The tendency is surprising when one considers that Whipple's (1927) widely-used manual describes methods of obtaining volumetric units when counting phytoplankton. It may be that the rather tedious methods described by Whipple have discouraged investigators, because Whipple's methods imply that the volume of every cell observed while counting should be computed. But it is only necessary to obtain dimensions of enough cells to provide a satisfactory estimate of average volume for the dominant species, then use these averages to convert "cells per liter" to "plant volume per litter." Indeed such a method can be more accurate than attempting to measure individuals in the counting chamber, because the measurements can be made under higher magnification, thus improving the estimates of average volumes.

Phytoplankton studies in western Lake Erie since 1948 have employed this method and crops have been expressed in volumetric units. Moreover, the measurements obtained make it possible to convert Chandler's (1940) units to volumetric units in many cases. For example, the maximal crop of diatoms reported by Chandler (1944) for the spring of 1941 was 10^6 units per liter, mostly *Asterionella,* of which 8 cells were regarded as a unit. The *Asterionella* usually encountered in western Lake Erie has a volume of about 720 μ^3 per cell, so the 1941 crop amounted to about 6 $mm.^3/1$. The crop of the spring of 1949, composed almost entirely of *Tabellaria,* was somewhat higher, amounting to about 16 $mm.^3/1$.

In Table II some maximal crops are shown for various habitats. Sanctuary Lake and Moriches Bay are shallow habitats, having mean depths of about 1.5 m. Crops of this magnitude probably represent the highest population densities one is likely to encounter in natural waters. Gessner (1949) reports chlorophyll yields of 1.34 $gm./m.^2$ for a duckpond of depth 2-3 dm. The chlorophyll concentration must have approximated 5 mg./1., and if the ratio of chlorophyll to organic matter was 0.01 the water may have contained 500 mg. of suspended organic matter per liter and a phytoplankton volume of 10^3 $mm.^3/1$.

The maximal crops in western Lake Erie, where depth is about 10 m., are about one-tenth as high as the upper limits apparent in Table II. Similar crops were computed from Marshall and Orr's (1930) data for Loch Striven. Their "cells per liter" were converted to volumes per liter using dimensions for *Skeletonema costatum* as given by Cupp (1943). Riley's data for phytoplankton over Georges Bank probably represent a fairly typical spring pulse in a relatively shallow (75 m.) marine habitat.

The ash-free dry weights are included in the table to show the relationship of this statistic to phytoplankton volume, but it should be noted that

TABLE II. *Maximal phytoplankton crops in various habitats*

Habitat	Crop per liter		Investigators
	mm.³	ash-free dry wt. (mg.)	
Sanctuary Lake	100*	27	Tryon and Jackson (1952)
Moriches Bay	100*	24	Ryther, Richards†
Gulf of Mexico "Red Tide"	100	..	Davis (1948)
Western Lake Erie	10	3	Chandler (1944), Verduin (1951a)
Loch Striven	10	..	Marshall and Orr (1930)
Georges Bank	2	0.5	Riley (1941)

*These data have been computed using dimensions provided by the investigators in private communications.
†Personal communication.

in the Lake Erie and Georges Bank data the estimates are based on net hauls, undoubtedly the ash-free dry weight of centrifuged samples of water containing such phytoplankton crops would be considerably higher, because an important fraction of the smaller suspensoids is lost by the net.

Chlorophyll concentration per liter, which has frequently been used as a measure of phytoplankton abundance, can be related approximately to the data in Table II by noting that Manning and Juday (1941) usually obtained ratios of 0.002-0.003 between chlorophyll and ash-free dry weight in Wisconsin lakes, although ratios as high as 0.059 were obtained. Riley's (1941) data show an average ratio of 0.0042 for six cruises over Georges Bank. His data represent net plankton; Manning and Juday concentrated phytoplankton with a centrifuge. Centrifuge samples probably contain more tripton than net samples and lakes probably contain more tripton than ocean waters. The average ratio of chlorophyll to dry weight in terrestrial plant leaves is about 0.01 (Spoehr 1926). Riley's data also provide an estimate of chlorophyll per unit of phytoplankton volume, amounting to 1.9 μg./mm.³

Some records of phytoplankton crops in volumetric units, appearing in the literature, seem too high. Apparently errors in computation have gone undetected. Thus, Edmondson and Edmondson (1947) reported phytoplankton volumes of 5 mm.³/ml., and they record chlorophyll concentrations of 16 mg./l. Both of these values seem too high by a factor of 10^3. In answer to a letter pointing out these facts, Edmondson states that the chlorophyll concentrations should be μg. (not mg.) per liter, and that loss of a decimal point before the figures in their graph accounts for a 10-fold discrepancy in the phytoplankton data; the remaining discrepancy may be attributed to the error of reporting directly the populations observed in the counting chamber, which represented a 100-fold concentration. And Brinley (1942a, 1942b) studying polluted portions of rivers reported populations as high as 58,000 parts per million. All his crops were of the order of thousands of parts per million. It seems likely that those values also should be reduced by a factor of 10^3, in which case his maximal values would be about five times higher than the maxima in western Lake Erie. An error of 10^3 is obviously present in Brinley's values for O_2 content of polluted waters; he reports minimal values of 667 p.p.m.

Ratios of ash-free dry weight to phytoplankton volume

Since 1951, the dry weight, and ash-free dry weight, of phytoplankton have been determined regularly on net samples obtained at about 2-hr. intervals (20 mi.) on each sampling cruise in western Lake Erie. The phytoplankton volume in these samples was determined also, so the data provide ratios of ash-free dry weight to phytoplankton volume, and of ash-free dry weight to total dry weight. Riley (1941) made similar determinations for marine phytoplankton collected on six cruises over Georges Bank. In Table III, Lake Erie data from eleven cruises representing spring, summer and fall seasons, are compared with average values for all six cruises of Riley.

TABLE III. *Ratios of ash-free dry weight to phytoplankton volume and to total dry weight: Lake Erie data compared with data for marine phytoplankton*

	Ratio of ash-free dry wt. to phytoplankton volume (mg./mm.³)	Ratio of ash-free to total dry wt.
Western Lake Erie eleven cruises	0.31	0.50
Georges Bank six cruises	0.45	0.64

The Lake Erie values are in close agreement with those representing marine phytoplankton. It should be noted here that even in net samples significant tripton fractions may be present, which tend to make these ratios too high. Note how far these ratios depart from what Ruttner (1953) calls "the generally applicable assumption that plankton contains approximately 90 per cent water" (p. 145). On the basis of that assumption the ratio of ash-free dry weight to phytoplankton volume (also assuming, as Ruttner does, that specific gravity of living phytoplankters is 1) would have to be less than 0.10.

An inspection of individual values in Riley's

publication shows that marked variations occurred from time to time. Thus, if the March and April data of Riley, which represent the maximal phytoplankton populations, are averaged the ash-free dry weight per mm.^{3} amounts to only 0.27 mg., and the ash-free dry weight represents 56% of the total dry weight. Similar variations appear in the Lake Erie data. For example: 4 samples collected on December 19, 1952, showed an average ash-free dry weight of 0.57 mg./mm.^{3}, and 4 samples collected on October 8, 1952, showed an ash-free dry weight fraction of 78% of the total dry weight.

The above ratios of ash-free dry weight to plant volume have an important bearing on the relationship between plankton organic matter and tripton in seston determinations. In a recent paper, Andrews (1953) contends that the "points on the organic seston curve are representative of the standing crop of plankton in Lake Erie," and he records a mean annual organic seston of 2.8 mg./l. for the Bass Islands region. Such an amount of organic matter would correspond to a mean annual standing crop of nearly 10 mm^3./l., a value close to the Lake Erie maxima listed in Table II. The mean annual standing crop, even in years when the spring maximum reaches such values, is less than half so high. The mean annual organic seston, therefore, must be more than half tripton. Andrews recognized that in exceptional cases, when the total seston was high (meaning that the water was excessively turbid) the organic fraction was largely contributed by tripton, but he failed to realize that the waters of the Bass Islands region contain a large tripton component at all times. The same can undoubtedly be said of many aquatic environments, and it should be realized that tripton has frequently been included with phytoplankton estimates. Birge and Juday (1922) included tripton organic matter in their "nannoplankton organic" and this error has undoubtedly resulted in a distorted concept of the general importance of nannoplankton. The error has been pointed out by Ruttner (1953: 145). Ruttner states that nannoplankton in alpine lakes, when estimated by microscopic examination, averaged only half as much as the net plankton. But even these estimates are somewhat ambiguous for the ratio of nanno- to net-plankton is largely a function of the hydrostatic pressure to which the net is subjected. This fact can be demonstrated by referring to the difference between results obtained in Lake Erie with a net as compared to a bolting cloth disk of the same material (see methods) in a community having an important *Cyclotella* component. With the disk, the hydrostatic pressure was kept at about 2 cm. of water, and the *Cyclotella* component was retained by the disk, but most of it was lost by the net. If the fraction lost by the net is regarded as nannoplankton, the ratio of nanno- to net-plankton in that community would be approximately 1. But if the fraction lost by the disk is regarded as nannoplankton, the ratio becomes much smaller. The nannoplankton concept, therefore, in its presently accepted form, is not a very useful one.

Summary

The highest phytoplankton crop observed in western Lake Erie between September, 1938, and September, 1953, was the spring crop of 1949 (16 mm.^{3}/l.). That crop was associated with transparencies permitting 1% of surface light to penetrate to 4.8 m. Only during one season in the period of study were large areas encountered exhibiting turbidities so high (1% of surface light at 3.5 m.) that they could be supposed to exert a major controlling influence on phytoplankton growth. The low spring crops of 1951-52-53 (1-2 mm.^{3}/l.) were associated with transparencies permitting 1% of surface light to penetrate to 6.6, 5.4, and 7.2 m. respectively.

Maps are presented showing the horizontal distribution of turbidities in an area comprising about half of western Lake Erie. The highest turbidities were found consistently in the Bass Islands region, with clearer waters to the northwest, northeast, and east. But waters to the northwest were consistently clearer than those to the northeast, indicating that turbid waters move northeastward through the Bass Islands region, mixing with clearer waters from the west and north, and leaving the western basin through the passage north of Pelee Island. This pattern is consistent with measurements of currents in channels north and south of Pelee Island. Net flow through the channel north of Pelee Island is outward and exceeds the total inflow of rivers entering the western basin; net flow through the channels south of Pelee Island is inward, preventing escape of western basin waters through these channels.

A graph of phytoplankton crops against the depth associated with 1% of surface light, constructed from data obtained during the spring of 1950, showed that the highest crops arose in waters of intermediate turbidity. It is suggested that the maximal phytoplankton crops, like that of 1949, may arise only when an influx of clear water driven by northeast winds, mixes with turbid, fertile waters in the Bass Islands region, creating large water masses having enhanced fertility plus sufficient transparency to promote utilization of the fertilizer by phytoplankton.

The effectiveness of light-quenching by sus-

pended particles in waters of the Bass Islands region has been determined by computing the value of k in an equation ($k = 4.6/d'c$) derived from the Lambert-Beer's Law using experimental determinations of the depth (d') associated with 1% of surface light, and the concentration (c) of suspended matter in the water. Values of k, in 35 samples, ranged from 0.10 to 0.20, when d' was expressed in meters and c in mg./l. (oven-dry). Of the 35 samples, 27 showed k values between 0.11 and 0.15.

A table of maximal phytoplankton crops from various habitats is presented, showing that the upper limits occurring in shallow habitats (1.5 m.) appear to be of the order of 100 mm.^{3}/l.

References

Andrews, T. F. 1948. Temporary changes of certain limnological conditions in western Lake Erie produced by a windstorm. Ecology **29**: 501-505.

———. 1953. Seasonal variations in relative abundance of *Cyclops vernalis* Fischer, *Cyclops bicuspidatus* Claus, and *Mesocyclops Leuckarti* (Claus), in western Lake Erie, from July, 1946, to May, 1948. Ohio Jour. Sci. **53**: 91-100.

Birge, E. A., and C. Juday. 1922. The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. Wisconsin Geol. and Nat. Hist. Survey. Bull. No. **64**.

Brinley, F. J. 1942a. The relation of domestic sewage to stream productivity. Ohio Jour. Sci. **42**: 173-176.

———. 1942b. The effect of the sewage from Nashville upon the plankton population of the Cumberland River. Jour. Tenn. Acad. Sci. **17**: 179-183.

Chandler, D. C. 1940. Limnological studies of western Lake Erie. I. Plankton and certain physical-chemical data of the Bass Islands region, from September, 1938, to November, 1939. Ohio Jour. Sci. **40**: 291-336.

———. 1942. II. Light penetration and its relation to turbidity. Ecology **23**: 41-52.

———. 1944. IV. Relation of limnological and climatic factors to the phytoplankton of 1941. Trans. Amer. Microsc. Soc. **63**: 203-236.

Chandler, D. C. and O. B. Weeks. 1945. V. Relation of limnological and meteorological conditions to the production of phytoplankton in 1942. Ecological Monog. **15**: 435-456.

Clarke, G. L. 1939. Variation in the transparency of three areas of the Atlantic throughout the year. Ecology **20**: 529-543.

Cupp, E. E. 1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Oceanog. **5**: 1-238.

Davis, C. C. 1948. *Gymnodinium brevis* sp. nov., a cause of discolored water and animal mortality in the Gulf of Mexico. Bot. Gaz. **109**: 358-360.

Edmondson, W. T., and Y. V. Edmondson. 1947. Measurements of production in fertilized salt-water. Sears Found: Jour. Mar. Res. **6**: 228-246.

Gessner, F. 1949. Der Chlorophyllgehalt im See und seine photosynthetische Valenz als geophysicalisches Problem. Schweiz. Zeitschr. f. Hydrologie. **11**: 378-410.

Lamar, W. 1953. Chapter 4, Lake Erie pollution survey, final report. Published by the Ohio Department of Natural Resources.

Manning, W. M., and R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in northeastern Wisconsin. Trans. Wisc. Acad. **33**: 363-393.

Marshall, S. M., and A. P. Orr. 1930. A study of the spring diatom increase in Loch Striven. Jour. Mar. Biol. Assoc. U. K., N. S. **16**: 853-878.

Riley, G. A. 1941. Plankton studies. IV. Georges Bank. Bull. Bingh. Oceanog. Coll. **7**: 4.

Ruttner, F. 1953. Fundamentals of limnology. (Transl. by D. G. Frey and F. E. J. Fry) Univ. Toronto Press.

Spoehr, H. A. 1926. Photosynthesis. The Chemical Catalog Co., Inc., N. Y.

Tryon, C. A., and D. F. Jackson. 1952. Summer plankton productivity of Pymatuning Lake, Pennsylvania. Ecology **33**: 342-350.

Verber, J. L. 1953. Rotational water movements in western Lake Erie. Proceedings Internat. Assoc. Limnology (in press).

Verduin, J. 1951a. A comparison of phytoplankton data obtained by a mobile sampling method with those obtained from a single station. Amer. Jour. Bot. **38**: 5-11.

———. 1951b. Comparison of spring diatom crops of western Lake Erie in 1949 and 1950. Ecology **32**: 662-668.

———. 1952. Photosynthesis and growth rates of two diatom communities in western Lake Erie. Ecology **33**: 163-168.

———. 1953. Baule-Mitscherlich limiting factor equation. Science **117**: 392.

Whipple, G. C. 1927. Microscopy of drinking water. 4th ed. John Wiley and Sons, Inc., N. Y.

Whitney, L. V. 1938. Transmission of solar energy and the scattering produced by suspensoids in lake waters. Trans. Wisc. Acad. **31**: 201-221.

THE ROLE OF THERMAL RADIATION IN ANIMAL ECOLOGY[1]

C. F. Kelly, T. E. Bond and Hubert Heitman, Jr.[2]
University of California, Davis, California

All things, both living and inanimate, attempt to come to a heat balance with their changing environment. Inanimate objects approach heat balance passively, their temperatures being uncontrollable. Mammals, on the other hand, must maintain their body or tissue temperatures within rather narrow limits in order to stay alive, and this type of balance requires that they adjust their rate of heat loss to their thermal environment. Animals differ widely in their ability to make this adjustment. Beef cattle of European breeds cannot usually live without shade in the summers of the Imperial Valley of California (Ittner and Kelly 1951). As to plants, Meyer and Anderson (1939) estimate that the radiant energy from the sun would be sufficient to heat most plant leaves to their lethal temperature in two minutes if as little as 50% of the energy were absorbed and none lost.

This paper discusses some of the results of a cooperative study by the U. S. Department of Agriculture and the University of California on the rate of heat loss from animals, with special reference to the role in the heat balance of radiation, as compared to convection, conduction, and evaporation.

Comparative Heat Balances

In addition to dealing with the heat load of their environment, mammals must dissipate about ⅓ of the total digestible nutrients of their feed as heat (Kleiber *et al.*, 1945). If they are not able to do so their body temperature rises and they attempt to reach a comfortable heat balance by cutting down on their feed intake, with a resulting slowing down of their rate of weight gain or production of milk, eggs, etc.

Comparative heat balances in the sun for an inanimate object and two living creatures are given in Fig. 1. A series of simultaneous observations —of the temperatures of a 6-inch globe thermometer, of English walnut leaves, and of a Jersey cow nursing a calf—are shown for a 12-hour daytime period. The globe thermometer reached a momentary balance with its thermal environment at a rather high level during the hottest part of the day, when the heat received from radiation equalled that lost by convection (Bedford and Warner 1934). Being inanimate it had no way of shifting its heat transference to vaporization or increased convection, but had to assume an equilibrium temperature.

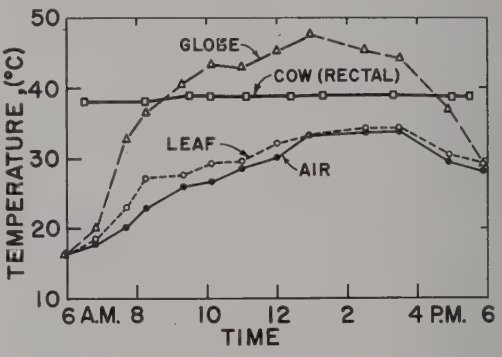

Fig. 1. Temperatures of 6-inch black globe thermometer, English walnut leaves, and Jersey cow, exposed to full sunlight on July 28, 1953, at Davis, California, as compared with air temperature.

The leaves came to a lower maximum temperature than the globe. They had a large surface area compared to their mass, a higher reflectivity for radiation, and auxiliary methods of increasing heat loss, such as evaporation and increased convection loss through leaf movement.

The cow also—even with a much smaller surface area per unit mass than either the globe or leaf had, and with a much greater metabolic heat, incident to milk production—was able to maintain a quite uniform body temperature throughout the day. It did this through two reactions: the rate of moisture evaporation from its lungs and nasal passages was increased, and its surface temperature became higher, thus increasing cooling by both convection and conduction. Its respiration rate increased from 49 breaths per minute at 8 a.m. to a high of 72 at 3 p.m., and then fell to a low of 28 per minute at 5:30. During the day the cow's surface temperature ranged from a low of 28° C. on the side in the shade at 6:30 a.m., up to

[1] All heat units are in terms of kilogram-calories, denoted "Calories."

[2] The authors wish to express great appreciation to Dr. F. A. Brooks and Professor R. L. Perry, of the University of California at Davis, for constructive criticism given in the preparation of this paper.

a high of 43° C. on the side in the sun at 12:30 p.m.

Importance of Radiation in Heat Balance

In this day of the radiant heating and cooling of homes, engineers in heating and air conditioning are fully aware of the part that radiation plays in supplementing the heat losses and gains of the human body through convection, conduction, and evaporation. The American Society of Heating and Ventilating Engineers (1950) has given radiation full equality with convection in establishing the rate of heat loss from the body. For instance, if we are comfortable in a room where the ambient temperature is 20° C. and the wall temperature the same, we will be about equally comfortable when the air temperature is lowered to 15° and the wall temperature increased to 25° C. A lowering of air temperature is compensated for by an equal and opposite change of wall temperature. The same conclusion has been reached by Raber and Hutchinson (1947).

Our studies of swine in the University of California psychrometric chamber (Heitman *et al.* 1949; Bond *et al.* 1952), over a temperature range from 4° to 38° C. (40° to 100° F.), have shown that when the temperature of the surroundings (walls, ceiling, and floor) was the same as the ambient air and the air motion was low (15 to 30 ft. per min.), heat-loss by radiation was practically the same as by convection. The results of a series of experiments with four hogs, weighing between 60 and 80 lbs., are shown in Figure 2. These animals were kept under conditions approaching those on a farm, being allowed freedom of movement and full rations of feed and water.

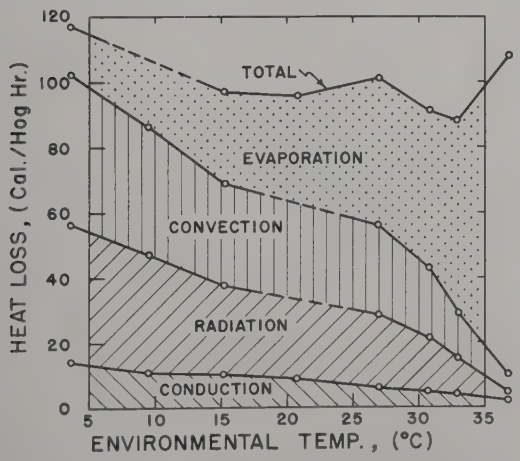

Fig. 2. Modes of heat loss by swine in thermal environment where air and surround temperatures were varied between 4 and 37°C.

The animals were maintained in uniform thermal environments for one-week periods, calorimeter measurements being made during the last three days at each temperature. Temperatures were varied with weekly changes of 10° F. (5.6° C.). The resulting changes in mode of heat loss are clear. Swine of this size are most comfortable and make the most efficient weight gains at environment temperatures ranging from about 21 to 27° C. (70 to 80° F.) (Heitman and Hughes 1949). As shown in Figure 2, in this "comfortable" environmental range the heat lost by the animal was almost equally divided among the three main modes—convection, radiation, and evaporation. Not much heat was lost by conduction: when the pigs were standing only a small area of their body was in contact with the floor; when they were lying down only about 20% of their body surface-area was thereby enabled to lose heat by conduction, and the heavily insulated floor of the chamber allowed little heat loss by this mode. Such loss might very well amount to more with an animal lying on cool, moist ground in the shade.

At the higher environmental temperatures more of the heat-load transfer was shifted to evaporation, as evidenced above 24° C. by a rapid increase in respiration rate. At the same time an increase occurs in the surface temperature of the animal, which of course directly affects the rate of heat losses by convection, radiation, and conduction. It will be remembered that the direction of heat-flow by these modes must always be from a region of higher to a region of lower temperature, and that the *rate* of flow is dependent upon the "potential," or difference in temperatures, between the two regions.

The surface temperature of homeotherms does not increase as fast as the environmental tempera-

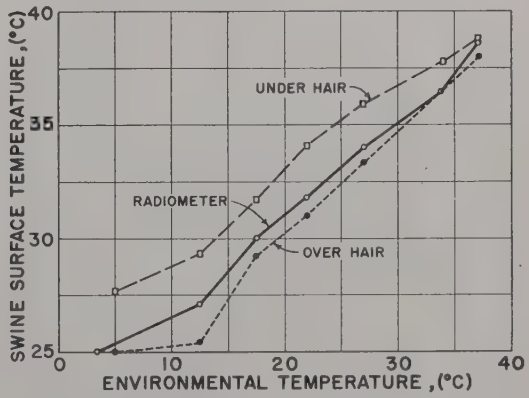

Fig. 3. Surface temperatures of swine at environmental temperatures ranging from 4 to 37°C., as determined by touch thermocouple and Hardy dermal radiometer.

ture, as shown by the curves for swine in Figure 3. These observations—shown here in average from 4 swine weighing between 180 and 260 lbs. —were made with a touch thermocouple and with a Hardy dermal radiometer. The touch thermocouple obtained two readings—the temperatures over the hair and the temperatures under the hair. Those under the hair, next to the skin, were of course the higher. The radiometer gave temperatures somewhat between the two thermocouple readings, since it "sees" both the outer ends of the hairs and some of the skin through the rather sparse swine bristles. In computing surface temperatures from emissive power observations the low temperature-emissivity of the hogs was taken as 0.93.

The "potential," which controls heat transfer by convection and radiation, decreased rapidly as the environmental temperature went up. Taking the radiometer reading as the single measure indicating heat transfer by both modes, we find that at 10° C. the potential is 16½°, at 20° it is 11¼°, at 30° only 5°, and at 38° the surface temperature of the hogs was the same as the environmental temperature, permitting loss only through evaporation.

Upper and Lower Hemisphere Radiation

The data given so far were obtained under controlled conditions, with the wall temperature (temperature of the "surround") being the same as the air temperature. Furthermore, the radiation from various solid angles of the sphere was rather uniform: the walls, ceiling, and floors all radiated to the hogs at about the same rate. (This is a condition seldom found in nature.)

Figure 4 shows the results of a series of traverses, with a Gier directional radiometer, in a plane extending in an east-west direction, up to the zenith and down to the nadir. The observations were made at noon on August 29, 1948, at El Centro, California. The left-hand section of Figure 4 shows the radiation environment of an unshaded animal; the right-hand section, that of a shaded animal. (The two environments actually are not as well defined as the diagram indicates, since the instrument has a cone of opening of 16°, causing some overlapping of the two sections.)

It will be noted that a point in shade, as on the right, receives radiation from five sources of varying intensity, as follows:

1. Cool, shaded ground.
2. Hot, unshaded ground.
3. Horizon (a band at ground level of about 10°).
4. Sky.
5. Hot shade surface overhead.

On the other hand an unshaded point, as on the left, receives radiation from only four sources: There is no cool, shaded ground, and the hot shade surface overhead is replaced by the hotter, direct sun.

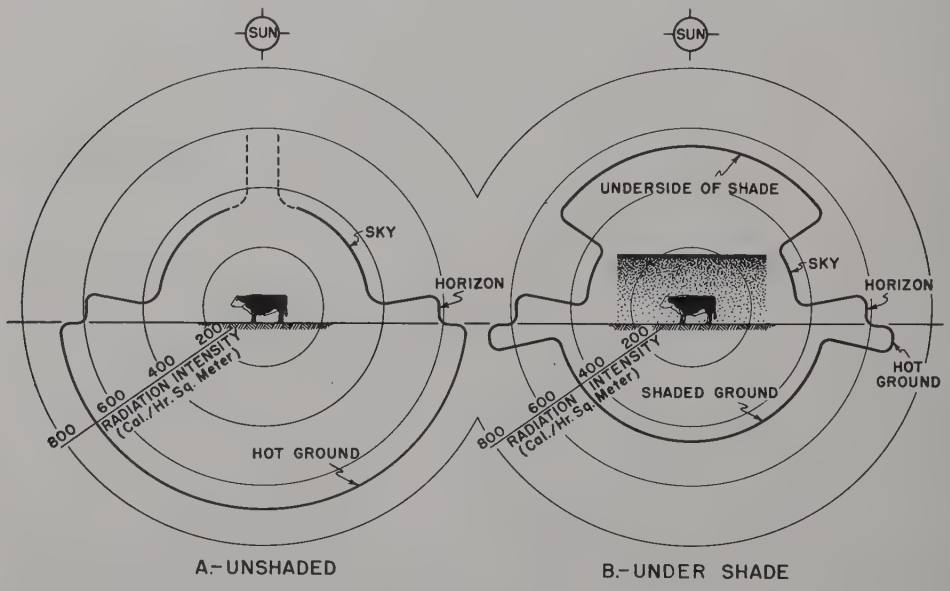

Fig. 4. Radiation intensity on shaded and unshaded animals on typical day at El Centro, California. Air temperature 40°C. Ground is bare. No clouds.

The relative importance of upper- and lower-hemisphere radiations is shown in the figure. Supplementary observations in the Imperial Valley, with a total-energy hemispherical black-plate radiometer, showed that standard cattle shades in that area lowered the radiation heat load on animals' horizontal backs by 50 to 65%. At the same time this instrument, when inverted, recorded a 25 to 30% reduction in lower-hemisphere radiation, due to the lesser radiosity of the shaded ground. Under such conditions an animal is subjected to about as much radiant energy from the lower hemisphere as from the upper. The exact ratio between the two will depend upon ground cover and type of shade, including its size, etc.

The animals tested under the conditions depicted in Figure 4 were Herefords, weighing about 750 lbs. each. The air temperature was 40° C., as was the surface temperature of the shaded animals. The temperature of the backs of the animals in the sun was 54.4°, of the sides 46°, and of the belly 43° C. An approximate heat balance indicated that the greater heat load on the animal in the sun would require it to lose by vaporization 339 more Calories per hour than the shaded animals—this despite the fact that its greater surface temperature would increase heat loss through convection.

Figure 4 also serves to illustrate several principles of shade construction:

1. The shade itself should be made of materials that will remain as cool as possible and will *not* have a reflecting undersurface.
2. The shade should be as high as practical, to expose the animals to as much cool sky and wind as possible.
3. The ground surrounding the shade should be planted to green grass. We have measured radiosity differences as great as 200 Calories/hr. sq. meter between black ground and green grass.

Solar and Atmospheric Radiation

The relation between an animal and its radiant surround may be conveniently studied under the following divisions: (1) the amount and quality of radiant energy reaching the animal; (2) the amount of energy reflected by the animal; and (3) the amount of energy absorbed by the animal.

Let us first consider the amount and quality of radiant energy reaching the animal from the upper hemisphere. Since radiant energy in transit consists of electromagnetic waves of greatly varying wavelengths, ranging from the very short cosmic rays through the ultraviolet and visible light rays to the long infrared and radio waves, radiation should be considered from the qualitative as well as the quantitative standpoint. The waves vary greatly in some of their effects. The band of visible rays, from 0.4 to 0.7 μ, affect the eye, allowing us to see; others, such as X-rays, are harmful to the human body when absorbed in excess. The only characteristic that all waves have in common—no matter what their wavelength—is that they produce heat when absorbed. All our heat energy originates at the sun, of course, and is transmitted to us by radiation. The nature of such radiation while still outside the atmosphere has been established. Since the sun radiates nearly as a black body, the monochromatic emission follows Planck's law. When radiant energy reaches the earth's atmosphere a large part is reflected by clouds or scattered back through outer space; a fraction is absorbed by the atmosphere; and the remainder is transmitted to the earth's surface—some as direct radiation, some as diffuse radiation. The wavelength of the energy is not changed by reflection or diffusion.

Most of the solar energy reaching the surface of the earth is absorbed by the ground. The earth radiates in turn to the sky. But since its temperature is much lower than the sun's the quality of radiaton is very different; instead of peak-radiation being at 0.5 μ it is at around 10 μ. On its outward trip toward space most of this "long wave" radiation is absorbed by water vapor, oxygen, CO_2, and other gases in the atmosphere. Brunt (1939) indicates that the atmosphere completely absorbs all energy between wavelengths of 5½ and 7μ and over wavelength of 14μ. There is partial absorption of energy between wavelengths of 7 to 8½ μ and 11 to 14 μ. None is absorbed between wavelengths of 8½ to 11 μ. The energy absorbed by atmospheric gases is in turn radiated back to earth or on to outer space. This is known as "atmospheric" radiation.

Thus the radiant energy reaching an animal from the upper hemisphere comes from three general sources: (1) direct solar radiation; (2) diffuse solar radiation; and (3) atmospheric radiation. Most discussions of radiation do not sufficiently emphasize atmospheric radiation.

The distribution of energy throughout the spectrum has not been measured. No one analysis could be accepted as showing the spectral distribution of energy radiated from the upper hemisphere, for it changes constantly with variations in cloudiness, the gas and vapor content of the air, the position of the sun, etc. Nevertheless a general analysis of radiation can be presented graphically so as to indicate approximately the various wavelengths (and amounts of each) that would

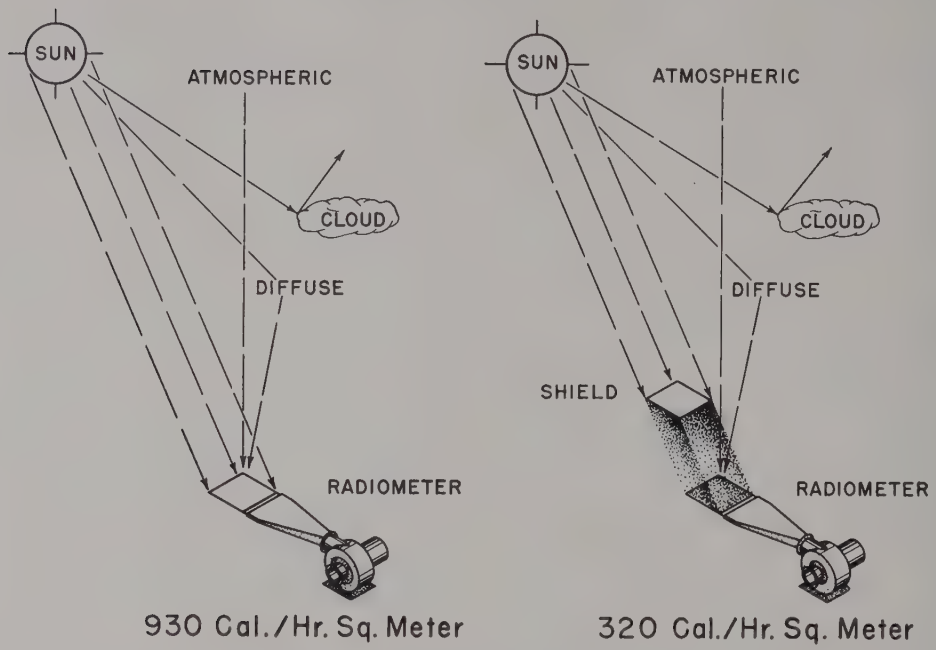

FIG. 5. Method of separating direct solar radiation from atmospheric and diffuse sky radiation by means of a small shield held over a total-energy hemispherical black-plate radiometer.

be incident upon an animal or other object. As shown in Figure 5, if a black-plate total-energy hemispherical radiometer is shaded by a small shield held several feet above the sensing element in such a way that the shape or angle factor of the shield with respect to the radiometer is so small as to be insignificant, the direct solar energy will be cut off, but a measurement of the combined energy from sky and atmosphere will be obtained. In the example shown the unshielded reading was 930 Cal./hr. sq. meter and the shielded 320. The difference between the two, 610 Cal./hr. sq. meter, is the short wave energy of the sun falling on a horizontal surface.

We have, then, two general "groups" of upper hemisphere radiant energy—one the solar energy, in the general region of 0.4 to 3 μ, amounting to 610 Cal./hr. sq. meter; the other the atmospheric radiation, in the general region of 3 μ to 50 μ, amounting to approximately 320 Cal./hr. sq. meter. (The diffuse solar radiation is included in the latter amount.) The value for the curves of Figure 6 were based upon these observations. The shape of the left-hand section of the curve, representing solar radiation, was developed from Abbot's (1937) table of the distribution of solar intensity by wavelength. These intensities are given in Abbot's table in arbitrary units, for an air mass path of 1 at sea level. By trial integration arithmetically several times, a value for the maximum intensity of 950 Cal./hr. sq. meter per μ at 0.5 μ was found where the area under the curve between 0.3 and 2.5 μ represented 687 Cal./hr. sq. meter. This value is 77 Cal. greater than the example, but the radiometer observation did not include short wave diffuse energy. This

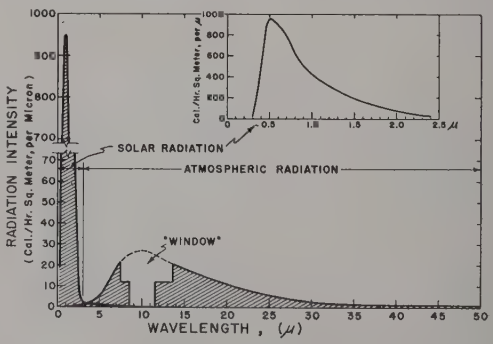

FIG. 6. Typical intensity of irradiation of horizontal surface by sun, sky and atmosphere, over spectrum 0.4 to 50 μ, at Davis, California. Insert chart is abscissa expansion over range 0.3 to 2.4 μ. This curve is based on Fig. 5, as explained in text.

77 Calories represents about 12% of the observed 610 Calories; Brooks (1952) considers that about ⅛ of solar radiation is diffuse.

On the right, the long wave section of the curve, representing atmospheric radiation, is based upon a Planckian curve for atmospheric and terrestrial radiation by Humphreys (1929), and upon the "window" concept by Brunt (1939). The area under the curve represents 243 Cals./hr. sq. meter, after subtracting the "window." The value of 243 Cals./hr. sq. meter is the incoming radiation, 320, minus the diffuse radiation, 77. The window, of course, represents the wavelengths in which the atmosphere is practically transparent. (By Kirchhoff's law the atmosphere cannot emit energy in the wavelengths to which it is transparent.)

Figure 6, then, represents the probable distribution of energy, by wavelengths, from 0.3 to 50 μ, for a particular condition, time, and place.

Reflectance and Absorptance of Swine

Radiant energy, before it becomes available for producing heat, must be absorbed. In studies of heat tolerance in farm animals the importance of the reflectance for solar energy of an animal's hair coat has been recognized for some time. The influence of the color of cattle's hair upon environment adaptability and energy-absorption has been studied by Bonsma (1943) and Riemerschmid and Elder (1945), in South Africa and Europe respectively, and by Rhoad (1940) and Brody (1948), in this country. The latest careful measurements, made by R. E. Stewart (1953), at the University of Missouri, gave definite values for the spectral reflectance of white, tan, black, and medium-red cattle coats for radiant energy between the wavelengths of 0.3 to 1.2 μ.

Swine differ from cattle in that their hairs are of greater diameter and fewer per unit of skin area. The skin color of swine also more closely matches that of the hair than in cattle. The spectral reflectance curves in Figure 7 were obtained on a General Electric spectrophotometer at the College of Engineering, University of California, Berkeley, by Louis Possner and J. T. Gier (private communication, 1949). Samples of skin with hair in place were used, since much of the skin can be seen through the sparse hair. The red skin was from a light-red Duroc-Jersey weighing about 150 lbs.; the black and white skins, from a Poland China hog weighing about 200 lbs. The wavelength range is from 0.4 to 1.0 μ. In general the reflectance values of given colors are quite close to those reported for cattle by Stewart (1953), the white animals reflecting about 75% of all energy with wavelength of 1 μ and the black animals

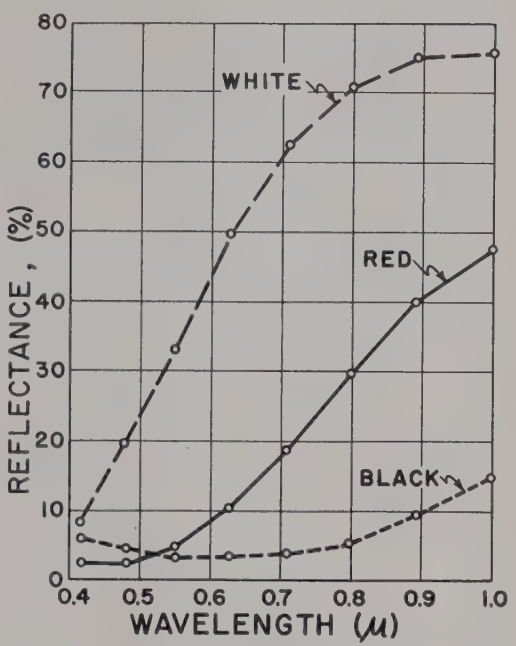

Fig. 7. Spectral reflectance of white, black, and reddish pig skin (hair in place) for radiant energy between wavelengths of 0.4 to 1.0 μ.

about 15% of the same wavelength. For shorter wavelengths reflectances drop off rapidly to approximately 10%.

The high reflectance of white animals for short wave energy would lead one to believe that they could easily exist in thermal environments where the black animals could not. The white pigs reflect 51% of solar energy between 0.4 and 1 μ while black pigs reflect only 7%. Although our observations in the field indicate that the lighter colored animals do have an advantage it certainly is not in proportion to this difference in spectral reflectivity. The reason is shown in Figure 8, where reflectance of black and white pigs for

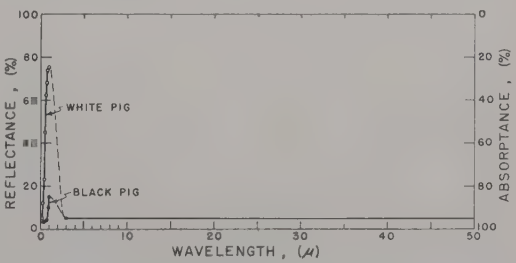

Fig. 8. Spectral reflectance and absorptance of white and black pigs for radiant energy between wavelengths of 0.4 to 50 μ.

energy ranging from 0.4 to 50 μ is shown. The data from 0.4 to 1.0 μ are taken from Figure 7. The data on reflectance for long wave energy, 3.0 to 50.0 μ, are based upon an average of the radiometer data shown in Figure 3 (regarding which it has already been said that the emissivity of pig skin, with hair, was taken as 0.93 in making the conversion to temperature) and upon Hardy's (1934) statement that the emissivity of human skin is about 0.98. (Possner and Gier, in a private communication, also report that pig skin has a low temperature-emissivity of "close to one" when examined with a two-barreled radiometer.) Since the value of 0.93 is apparently a little low, we have used 0.955, an average of these two values, as the emissivity in preparing Figure 8. The absorptivity of an opaque object is numerically the same as the emissivity, and reflectance is equal to one minus the absorptance. Because present equipment at the University cannot measure the spectral reflectance of combustible material, such as pig skin and hair (because of the high heat developed), we have interpolated values between 1 and 3 μ for reflectance. This assumption appears reasonable because (at least in the case of the white pig) reflectivity had already started to lower at a wavelength of 1 μ.

The *total* amounts of radiant energy absorbed by the horizontal planes of white pigs and by black pigs are compared, wavelength by wavelength, between 0.4 and 50 μ, in Figure 9. These absorption curves were developed by multiplying the radiation intensity at a given wavelength, as shown in Figure 6, by the absorptance at the same wavelength, as in Figure 8. The integrated value of energy absorbed over the range 0.4 to 3 μ is 331 Cal./hr. sq. meter for the white pig and 629 for the black pig. The black pig absorbs 90% more energy than the white pig between these limits. Over the range from 0.4 to 50 μ the white pig absorbs 585 Cal./hr. sq. meter and the black pig 883, only 50% more than the white pig. And if the two pigs were in shade, where all but a small part of the radiant energy would be in the long-wave infrared region, there would be little difference between the amounts absorbed. The difference between energy absorbed by white and black pigs in direct sunlight may be even less than indicated, as it is probable that the spectral reflectance of black pigs does not start to lower until a wavelength higher than 1 μ is reached.

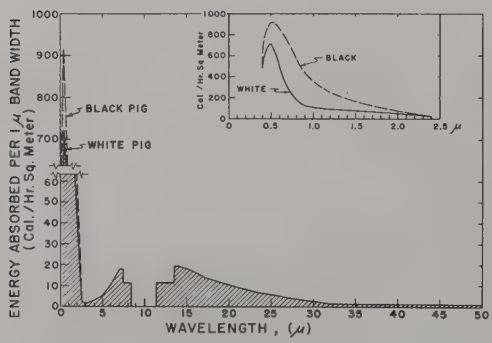

FIG. 9. Solar and atmospheric radiant energy absorbed by black and white pigs, by wavelengths, for typical atmospheric conditions at Davis, California. Insert diagram is absorption for solar radiation, range 0.4 to 2.4 μ, abscissa expanded.

SUMMARY

It was shown in the foregoing discussion that quality of incident radiation, together with reflectance characteristics of an animal surface, will determine what percentage of the total incident energy will affect the animal. For a true interpretation of the role of thermal radiation as an ecological factor one must consider quality as well as quantity of radiant energy.

Emphasis heretofore has been directed mainly toward the solar energy reaching the earth. It should be remembered that, while the solar beam short wave portion of the energy constitutes about 66 per cent of the total reaching the earth's surface, this energy comes from what is essentially a point source so that it shines on less than half the area of a solid object. Only a very small area of a cylindrical animal, such as a pig, ever meets such conditions as outlined in this paper, the worst possible exposure to upper hemisphere radiation, with the sun directly overhead. At least half the surface will never be exposed to direct solar radiation, and most of the half exposed will be at such "grazing" angles that the energy per unit area will be very much decreased.

On the other hand, the long wave portion and diffuse solar radiation emanates from a hemispherical source thousands of times greater than the sun's disk and irradiates a much larger area of the solid object or animal.

This analysis should lead to a better basic understanding of the role of thermal radiation in animal ecology.

REFERENCES

Abbot, C. G. 1937. Measurement of radiant energy—the sun as a source of continuous radiation. New York: McGraw-Hill.

American Society of Heating and Ventilating Engineers. 1950. Heating, Ventilating, Air Conditioning Guide. Published by the Society, 51 Madison Avenue, New York.

Bedford, T., and C. G. Warner. 1934. The globe thermometer in studies of heating and ventilation. Journal of Hygiene, **34**: 458.

Bond, T. E., C. F. Kelly, and Hubert Heitman, Jr. 1952. Heat and moisture loss from swine. Agricultural Engineering, **33**: 148-152.

Bonsma, J. C. 1943. Influence of colour and coat cover on adaptability of cattle. Farming in South Africa, February, 1943.

Brody, S. 1948. Environmental physiology with special reference to domestic animals. Missouri Agri. Exp. Sta. Res. Bulletin 423.

Brooks, F. A. 1952. Atmospheric radiation and its reflection from the ground. Jour. of Meteorology, **9**: 41-52.

Brunt, David. 1939. Physical and dynamical meteorology. New York: Cambridge University Press.

Hardy, J. D. 1934. The radiation of heat from the human body. Jour. of Clinical Invest., **13**: 817.

Heitman, Hubert, Jr., and E. H. Hughes. 1949. The effects of air temperature and relative humidity on the physiological well being of swine. Jour. of Animal Sci., **8**: 171-181.

Heitman, Hubert, Jr., C. F. Kelly, and E. H. Hughes. 1949. California psychrometric chamber for livestock environment studies. Jour. of Animal Sci., **8**: 459-463.

Humphreys, W. J. 1929. Physics of the air. New York: McGraw-Hill.

Ittner, N. R. and C. F. Kelly. 1951. Cattle shades. Jour. of Animal Sci., **10**: 184-194.

Kleiber, Max, W. M. Regan, and S. W. Meade. 1945. Measuring food value for dairy cows. University of California, Hilgardia, **16**: 11.

Meyer, B. S., and D. B. Anderson. 1939. Plant physiology. New York: Van Nostrand (Ref., p. 167).

Raber, F. B., and F. W. Hutchinson. 1947. Panel heating and cooling analysis. New York: Wiley.

Rhoad, A. O. 1940. Absorption and reflection of solar radiation in relation to coat color in cattle. Proc. Amer. Soc. Animal Prod., **33**: 291-293.

Riemerschmid, G., and J. S. Elder. 1945. The absorptivity for solar radiation of different colored hairy coats of cattle. Onderstepoort Jour. Vet. Sci. Animal Ind., **20**: 223-234.

Stewart, R. E. 1953. Absorption of solar radiation by the hair of cattle. Agricultural Engineering, **34**: 235-238.

AN EXAMPLE OF LONG DISTANCE DISPERSAL

B. W. Taylor[1]

Botany Department, Sydney University, Sydney, N.S.W., Australia

There are numerous species known to have wide discontinuities in their distribution. Most of these can readily be explained in the light of our knowledge of past climatic fluctuations and of changes in the relationships of land to sea. There still remains a small minority of species whose pattern of distribution lacks a convincing explanation. The concept of long distance dispersal of seeds and fruits has been applied to many of these species but has so often proved unconvincing that the theory is now frequently dismissed. This paper attempts to present the evidence on the origin of a small oceanic flora, that of Macquarie Island—evidence which points very strongly to long distance dispersal.

Introduction

Macquarie Island (54°S, 157°E), a base of the Australian National Antarctic Research Expedition, is a small sub-antarctic island far distant from any large land mass and surrounded by ocean exceeding 2,000 meters in depth. It lies 950 km. southwest of New Zealand, 1,300 km. southeast of Tasmania and 6,500 km. from South America. The nearest islands are the Auckland and Campbell groups, both of which are approximately 650 km. to the northeast.

The vascular flora consists of only 35 species. Three of these species are endemic to the island, the remainder are distributed on various patterns, being also recorded from New Zealand, South America, and other sub-antarctic islands. It is noteworthy that 4 of the species are found in South America but are not recorded from New Zealand or the Auckland and Campbell groups, a discontinuity of 4,000 miles.

The climate of Macquarie Island is cold, wet, and windy. The mean temperature is 4.5°C with an exceedingly small monthly range, from 3° to 6°C, with an absolute maximum of 11.0°C. The annual precipitation is 130 cm., which is spread over 340 rainy days per year. The wind averages 25 km. per hour with gusts of gale force on 180 days per year.

The island is of volcanic origin, probably emerging during the Cretaceous Period (Mawson 1943), and consists of basic igneous rocks, sedimentary rocks being absent. During the Pleistocene Epoch, the island was covered by a thick ice

[1] The data presented in this note were collected while the author was Biologist with the Australian National Antarctic Research Expedition, under the leadership of Mr. P. G. Law. Grateful thanks for helpful criticism and discussion are due to Dr. N. C. W. Beadle, Mr. S. Smith-White, and Dr. J. McLuckie of the Botany Department, Sydney University.

sheet. There is abundant evidence of this ice sheet, but there is no geological evidence of any ice-free land in the area during the glacial period. All mountains and ridges have been worn smooth by the action of the ice sheet and there are no knife-edge peaks indicative of nunataks on which flowering plants may have survived.

The Case for Long Distance Dispersal

It seems unlikely that the 35 species could have survived this severe glaciation even if there were ice-free areas. The majority of species are absent today from the higher ridges where the climate is slightly more severe. Further, vascular plants are absent today from glaciated Antarctic islands, *e.g.*, Bouvet Island, South Orkney Islands, South Sandwich Islands, and Balleny Islands. Two species, *Deschampsia antarctica* E. Desv. and *Colobanthus crassifolius* Hook. f., have been recorded from the heavily glaciated South Shetland Islands, but these are very rare and reproduce only vegetatively. These two species are presumed to be recent immigrants from South America (Brown 1927). With sub-antarctic islands, the number of species present is related to the mean temperature and the isolation of the island. This can best be explained by a consideration of the difficulties of immigrant species reaching the island.

At least one species, *Myriophyllum elatinoides* Gaudich., found today on Macquarie Island, could not have survived there during the glacial period. This species is an obligate aquatic and could not survive in perennially frozen lakes. Under present-day conditions on the island, it reproduces only vegetatively, though in New Zealand and South America the same species flowers and fruits normally. Thus, this species must be a post-glacial immigrant, and once allowing the possibility of immigration, it is only logical to apply it to other species where evidence favors such immigration.

Method of Immigration

Immigration may have occurred in several ways. Theories of continental drift and land bridges would permit an explanation of the migration of the flora with only short dispersal steps. However, it is untenable that such major geographical changes could have occurred since the recession of the ice sheet less than 20,000 years ago. Moreover, since the melting of the ice, Macquarie Island has been rising (Mawson 1943), and it is unlikely that any land of a postulated land bridge would have sunk, certainly not to a depth of 2,000 meters.

There remain only such migration theories that permit of dispersal over long distances, possible agencies being air and sea currents, and migratory animals. It may be that the strong westerly winds that ring the globe between 40° and 60°S could have resulted in the establishment of some species with minute seeds. However, they could not explain the presence of the great majority of species which have relatively large seeds. Similarly, sea currents which come from the west and north might have brought seeds to a suitable habitat on the island, but this would involve immersion in cold sea water for periods of at least a year.

Neither of these agencies can be dismissed as a possible explanation of the immigration of some species but a much more probable explanation lies in the myriads of sea birds which inhabit the island. These birds make long flights to South America, New Zealand, and to other sub-antarctic islands. Most of the birds vacate Macquarie Island in winter and are recorded by ships far from land. Despite the small number of birds tagged, several instances of long individual flights are known, *e.g.*, a giant petrel released on Macquarie Island in 1950 was shot four months later on South Georgia, another sub-antarctic island 8,000 km. away.

All the vascular species have propagules suited to bird transport. The majority have seeds less than 1 mm. in length. The remainder have such structures as hooks, barbs, and bristles whilst one species *Coprosma pumila* Hook. f. has a sticky berry and another species, *Stilbocarpa polaris* A. Grey, has a relatively large (5 mm.) but very hard fruit which might pass undamaged through a bird.

An observation which overcomes many of the objections to the theory of long distance dispersal of seeds by birds, was made on Macquarie Island by an amateur naturalist, N. Laird, in 1948. He observed several small unidentified seeds and one fruit of *Stilbocarpa polaris* adhering to the feet of several black-browed albatrosses. These birds, in common with most sea birds, regurgitate an oily fluid when building nests and as a means of defence against intruders. This fluid on drying had encased the seeds noted. In such a condition seeds could be carried almost indefinitely in flight and could withstand immersion in sea water if the bird alighted to rest, yet on landing the seeds would be easily rubbed off.

Another seed, as yet unidentified, was found in 1951 by J. Bunt (full details in Taylor in press). This seed is quite distinct from that of any species known from the island. Despite the fact that the island has now been closely explored botanically, this seed may belong to a species present, but as yet unrecorded. It is equally possible that the seed was brought to the island by a bird, for

it was found on the shore of a highland lake which is inhabited by the largest flock of giant petrels on the island.

Objections to the Theory of Long Distance Dispersal

Objections to bird dispersal of seeds include suggestions that birds do not eat before migration, and the limits set by the time taken for a seed to pass through the digestive tract. However, many of the birds reaching Macquarie Island have migrated accidentally being borne away from other areas by sudden strong winds. This is shown by the appearance of stragglers from the New Zealand avifauna following the rare storms from the northeast. These winds reach velocities of 130 km.p.h. and more, so that 650 km. flights from the Auckland and Campbell groups need only be of short duration. *Coprosma pumila* and *Stilbocarpa polaris,* the only species adapted to internal carriage by birds, are both found in these closer islands. Both, however, could well be carried in another manner; the former adhering to a bird's beak, the latter, as already mentioned, adhering to a bird's foot.

Other objections have been raised to the general theory of long distance dispersal, notably by Cain (1944). Firstly he points out the difficulty of an immigrant species entering a closed community of established plants closely adapted to the local environment. This is not the case on Macquarie Island since half its area is covered by an open sub-glacial community where competition between individual plants is at a minimum. Moreover most species are not closely adapted to many of the diverse ecological niches they occupy. Thus, some species reproduce sexually only in a few microhabitats and elsewhere survive only because better adapted species are lacking. Thus, there are many sites with low competition in which an immigrant species could readily establish itself. The success of three exotic species, *Stellaria media* Cyr., *Cerastium triviale* Link., and *Poa annua* L., accidentally introduced by man, illustrates this point. On the more isolated island of Kerguelen, exotic species have been even more successful and now outnumber the native flora of 27 species.

Secondly, Cain stated that the high degree of endemism, which is related to the extent and age of isolation in islands, mountains, etc., is opposed to the concept of long distance dispersal. The proportion of endemics on Macquarie Island is high (9 per cent), but it cannot be compared with such islands as Hawaii, which has over 80 per cent endemics. Moreover two of the endemics on Macquarie Island, *Poa hamiltoni* T. Kirk and *Deschampsia penicillata* T. Kirk, have very close relatives on the island, namely *Poa foliosa* Hook f. and *Deschampsia chapmani* Petrie. Between these species pairs, there are striking vegetative and floral similarities. So close is the resemblance between *Poa hamiltoni* and *P. foliosa* that a field determination always needs confirmation from the structure of the ligule.

The most probable explanation for the evolution of the endemic *P. hamiltoni* is that a seed of the more widespread *P. foliosa* reached the island soon after the recession of the ice sheet. Under the conditions prevailing, that is, low competition and a small population, accidental genetic drift took place at a rapid rate. By the time a second seed of *P. foliosa* reached the island the two populations would not cross. A similar explanation would explain the origin of *Deschampsia penicillata* from *D. chapmani,* whilst the third endemic, *Puccinellia macquariensis* Cheesem., is probably derived from one of several closely related species of *Puccinellia* found on the Auckland, Campbell, and Antipodes groups.

In the colder sub-antarctic islands, the proportion of endemics rapidly drops to nil (full details in Taylor in press.). The most probable explanation of this is that decreasing mean temperatures, which implies less time since glaciation, would not allow sufficient time for speciation in post-glacial immigrants.

A third objection raised by Cain is that there are so many specific parallels throughout the world that long distance dispersal cannot reasonably be generally applied. However, the geological history of the sub-antarctic islands is markedly different from the world in general, in that they have been recently devastated by an ice age and since then there has been no other possible means of recolonization. In the Northern Hemisphere, plants could migrate into previously glaciated areas along continuous land, and as soon as ecological conditions permitted, could establish a closed community. Thus, the chance of an immigrant species becoming established would be greatly decreased.

Moreover, the floras of the sub-antarctic islands differ in one respect from the world in general. Good (1947) has listed 47 cosmopolitan genera, defined as genera present on all five continents. The floras of the more isolated sub-antarctic islands, Macquarie, Kerguelen, Heard, Marion, Crozets and South Georgia, have between 45 per cent and 65 per cent of their species belonging to these genera, the less isolated Falkland, Auckland and Campbell Islands have between 30 per cent and 40 per cent, while comparable continental areas and continental islands such as Stewart Is., New

Zealand, Patagonia, and Terra del Fuego have only 20-25 per cent of their species belonging to these genera. This discrepancy between continental areas and oceanic islands in the sub-antarctic zone can best be explained on the basis that species of cosmopolittan genera are generally better adapted to rapid dispersal than other species.

Cain argues further that the element of chance involved in long distance dispersal is so high that it cannot generally operate. Skottsberg (1905) arguing against long distance dispersal operating on South Georgia Island, states that if it were operative, then the flora would be much greater than it is today. These two arguments are contradictory and the truth would seem to lie between the two, especially when it is remembered that the chance of a species becoming established on a sub-antarctic island is greatly enhanced by the low competition from other species. It is only necessary for a single seed of a perfect-flowered or a monoecious species to grow for that species to enter the flora. In this regard, it is interesting to note that *Coprosma pumila* dioecious elsewhere in its range, has many individuals, if not all, on Macquarie Island which are monoecious.

Conclusion

The recent geological history of Macquarie Island, the trends in the numbers of species on sub-antarctic islands with isolation and decreasing mean temperature, the nature and proportion of endemic species, the high proportion of species of cosmopolitan genera and the low interspecific competition all point to the fact that the flora of Macquarie Island is composed of post-glacial immigrants. A probable mechanism for this migration lies in the myriads of sea birds which inhabit the island, a hypothesis not inconsistent with the nature of the propagules of all species found on the island.

If long-distance dispersal has occurred on Macquarie Island, then it could well have occurred elsewhere. Therefore it must be considered when dealing with floras of those areas, isolated by long-distance barriers from the centre of origin of the angiosperms or formed by volcanic or coral activity in a more recent geological period. These areas would present undeveloped habitats for the first migrants, but as each new species became established competition would become keener until the entry of an additional species would be very difficult and consequently of rare occurrence. Isolation of long duration would then permit the building up of a high proportion of endemic species. Thus, a consideration of the flora of Macquarie Island indicates that long-distance dispersal is a factor in species distribution and should be considered when studying the origin of a flora which has been isolated at any period during its history.

Summary

1. The position, climate, flora, and geological history of Macquarie Island are described.

2. The improbability of any species surviving the Glacial Epoch on Macquarie Island is pointed out.

3. Observations supporting bird dispersal of seeds are given.

4. Objections to the theory of long distance dispersal are discussed and the conclusion reached that long distance dispersal has occurred on Macquarie Island.

References

Blake, S. F., and A. C. Atwood. 1942. Geographical guide to the floras of the World, Part I. U. S. Dept. Agr. Misc. Publ. **401**.

Cain, S. A. 1944. Foundations of plant geography. Harper and Sons, New York.

Good, R. 1947. Geography of the flowering plants. Longmans, Green and Co., London.

Mason, D. 1943. Geography and geology of Macquarie Island. Australian Antarctic Expedition Repts. Series A, **5**.

Rudmose Brown, R. N. 1927. The polar region. Methuen and Co., London.

Schenck, H. (1906) Die Gefässpflanzen der Deutschen südpolar-expedition 1901-1903. Deutsche südpolar-expedition, **VIII** Band, Botanik, p. 97-123. Berlin.

Skottsberg, C. (1905) Die Gefässpflanzen Südgeorgiens. Wissen-schaftliche Ergebnisse der Schwedischen südpolar-expedition 1901-1903, Band **4**, Teil 10.

Taylor, B. W. The flora, vegetation and soils of Macquarie Island. Australian National Antarctic Research Expedition Repts. Botany, **1** (in press).

NOTES AND COMMENT

AN EXPLANATION FOR THE DISTRIBUTION OF A NORTH AMERICAN CRAYFISH

The discontinuous distribution of the crayfish *Orconectes neglectus neglectus* (Faxon) is one of the most perplexing problems offered by the crayfishes of the western Mississippi Valley. Today this subspecies is localized in three areas (Fig. 1). The main population is distributed over a large area in the headwaters of the White River in southwestern Missouri and northwestern Arkansas, and in the eastern tributaries of the Neosho River in northeastern Oklahoma, southeastern Kansas and southwestern Missouri. A second population occupies tributaries of the Kansas River in east-central Kansas (Wabaunsee and Riley Counties). The third population, recently found to occupy Rock Creek, a tributary of the Arikaree River in extreme southwestern Nebraska (Dundy County), was formerly reported from northwestern Kansas (Cheyenne and Decatur Counties, Republican River drainage) and from northeastern Colorado (Yuma and Sedgwick Counties, Republican and South Platte River drainages). The sole companion subspecies, *O. n. chaenodactylus* Williams, is found in the North Fork of the White River in Arkansas and Missouri. Extensive recent collections in Arkansas, Kansas, Missouri and Oklahoma (Williams and Leonard 1952; Williams, in press) and relatively recent work in Nebraska (Engle 1926) have not shown *O. n. neglectus* to be present in any of the streams between the three areas. (Two isolated records of the species in the Red River drainage of southern Oklahoma and northern Texas are not considered in this paper.)

Certain observed environmental factors in the places occupied by *O. n. neglectus* perhaps give a clue to its survival in the three areas. The subspecies is found in rocky or gravelly streams which contain clear water or at least water which is not continually laden with silt. Such streams are common in the Ozark Mountains. Individuals have been collected in streams from open water, from under rocks and from shallow burrows under rocks, but never from muddy burrows in stream banks nor from standing water in ponds or ditches. Mill Creek, Wabaunsee County, Kansas, the type locality for *O. n. neglectus,* is a clear stream running over limestone boulders and chert gravel through most of its length, but the stream is silty where it crosses the alluvial plain of the Kansas River. The area drained by this stream and other similar streams in the immediate vicinity is predominantly grassy range land. The subspecies is found in the upper reaches of these streams, but has not been found in the muddy lower stretches. The small population known to occur in Rock Creek, Dundy County, Nebraska, exists under conditions which are extraordinary in that region. This rocky, clear, spring-fed stream is cold enough to support an introduced population of trout. No other stream in this region has these characteristics. (Personal communication from Dr. Frank B. Cross and J. Knox Jones who with Olin L. Webb collected specimens of *O. n. neglectus* for the University of Kansas Museum of Natural History.) Other streams in this region from which the subspecies was formerly reported, and from which collections exist, are chiefly broad sandy streams which often become dry during protracted droughts.

The taxnomic relationships of *O. n. neglectus* (Ortmann, 1905) indicate that the central population of the subspecies is, and was, the Ozarkian population. The fact that no population of this subspecies now exists in the northern watershed of the Ozarks, in which there are abundant suitable habitats, seems to preclude the idea that the subspecies ever occupied these streams and from them worked up the Missouri and Kansas River Valleys to the areas occupied at present. Furthermore, if the subspecies had migrated upstream through the Missouri and Kansas River Valleys, small populations could be expected to occur in the rocky tributaries of the Kansas River which occur between Wabaunsee County and the mouth of the river. Many of these streams are spring-fed. The apparent intolerance of the form to silting makes migration over this route seem unlikely.

An alternative theoretical explanation of the present distribution was first mentioned to me by Professor A. Byron Leonard of the University of Kansas and is supported by knowledge of the Pleistocene drainages in Kansas (Frye and Leonard 1952). During early and middle Pleistocene (Nebraskan and Kansan times) a large drainage system flowed east and south through central Kansas. The south central portion of this system followed approximately the present course of the Arkansas River (Harvey, Sedgwick and Summer Counties) and continued into Oklahoma. The southern outlet of this system is unknown, but presumably it followed the course of the Arkansas River, connecting with streams that drain the western Ozark area occupied by *O. n. neglectus* today. From the north this central drainage flowed through McPherson County in a channel now filled and buried (McPherson Valley). From the north and east through Saline, Dickinson, Geary and Riley Counties the drainage followed approximately the present course of a segment of the Smoky Hill River. Water flowing through this last-named segment was outwash from the melting Kansan glacier, and the direction of flow was southwestward, the opposite of today. Other streams from the north, also outwash streams, fed into the system and parts of these streams formed connections with the present day Republican River system.

At one time in mid-Pleistocene a central Kansas drainage either simultaneously or progressively connected all the areas occupied by *O. n. neglectus* today. At that time it was possible that this subspecies of crayfish could have had a continuous distribution from the southwestern Ozarks throughout this drainage system. With the retreat of the Kansan glacier the flow of water in the eastern Smoky Hill River was reversed and concurrently the Kansas River came into being. Later in Illinoian time the McPherson Valley was filled and buried, presumably cutting off the Great Plains segment of *O. n. neglectus* from its Ozarkian center.

Before the plains were brought under cultivation by European immigrants, the streams of Colorado, Kansas and Nebraska were no doubt less heavily laden with silt than they are today. Until that time *O. n. neglectus* may have had a much wider distribution in the Republican River drainage, and even in the South Platte River drainage, than it does at present. The surviving plains pop-

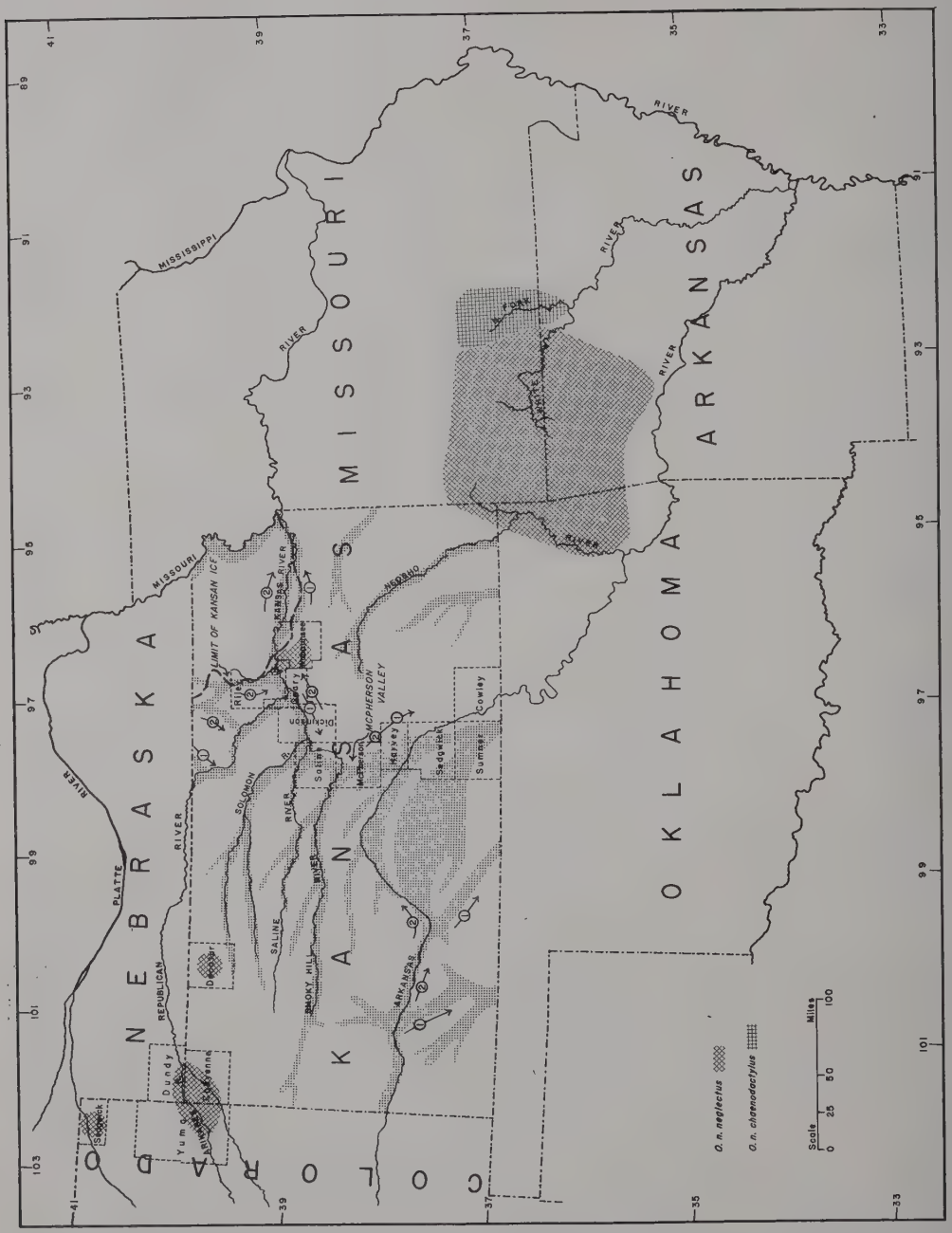

FIG. 1. Distribution of *Orconectes neglectus* subspecies in parts of six states. Existing major streams are shown superimposed by reconstructed major drainage paths in Kansas in late Kansan time. Numbered arrows refer to direction and position of stream flow during early stage of Kansan glacial retreat (1), and during late stage of Kansan retreat, or during early Yarmouthian time (2). Heavy dashed line is maximum limit of Kansan glacier. McPherson Valley is now abandoned. (Adapted from Frye and Leonard, 1952.)

ulations remain only in areas that are relatively undisturbed.

Summary

Environmental preferences apparently restrict the crayfish *Orconectes n. neglectus* to relatively clear rocky streams in the southwestern Ozark Mountains, and to small isolated populations in east-central Kansas and extreme southwestern Nebraska. The Pleistocene drainage pattern in Kansas provided the species with a possible avenue of distribution over the plains, but heavy silting of streams since the plains were brought under cultivation may have produced the existing restricted populations.

References

Engle, Earl Theron. 1926. Crayfishes of the genus *Cambarus* in Nebraska and eastern Colorado. Bull. U. S. Bur. Fish., **42**: 87-104.

Frye, John C. and A. Byron Leonard. 1952. Pleistocene geology of Kansas. Univ. Kansas Pubs., State Geol. Surv. Kansas. Bull. **99**: 1-230.

Ortmann, A. E. 1905. The mutual affinities of the species of the genus *Cambarus,* and their dispersal over the United States. Proc. Amer. Philos. Soc., Philadelphia, **44**: 91-136.

Williams, Austin B. (In press.) Speciation and distribution of the crayfishes of the Ozark Plateaus and Ouachita Provinces. Univ. Kansas Sci. Bull.

Williams, Austin B. and A. Byron Leonard. 1952. The crayfishes of Kansas. Univ. Kansas Sci. Bull. **34**, Pt. 2: 961-1012.

Austin B. Williams

Institute of Fisheries Research

University of North Carolina

Morehead City, North Carolina

CLIMAX VEGETATION AND THE REGIONAL SHIFT OF CONTROLS[1]

In an effort to reach beyond the semantic screen which surrounds much discussion on the nature of the climax, I would like to set down a few ideas which I think are particularly relevant at this time. This is just a preliminary note and makes no attempt to distribute credits and to review the abundant literature. It focuses upon the alignment of environmental forces (climatic and edaphic) as it appears to us in various parts of the world, and it proposes a general scheme in interpretation. The latter was first presented in Philadelphia at the 1951 meetings of the American Association for the Advancement of Science. It has been developed more fully and documented extensively in a lengthy paper which will bear the title "L'efficacité du climat et les inhibitions édaphiques" probably to be published next year in the "Acta Biotheoretica."

The very few examples and citations offered here have been chosen with the sole view of making my meanings more concrete, and not as a reference to the earliest, best, or most original contribution to be quoted in reference to a particular point.

The Question of Climax

It has been widely held by field workers in various parts of the world that the combined forces of climate, soil, and vegetation *tend* towards a dynamic equilibrium, the climax. This plant community, occurring on upland, has the power to perpetuate itself essentially unchanged, as long as the climate remains what it is (Clements 1936, Cain 1939).

This view has been opposed because of the known confinement of many plants to certain geological substrata; the lags of soil formation; the vagaries of dispersal; the fluctuations of climate; the rates of geomorphic change; the great durability of other plant communities; the inconsistency of all plant communities. In other words a strict and universal application of the climax theory would seem to take for granted a number of unproven tenets not only concerning the relation of vegetation to landscape but also the "reality" of almost any basic phytosociological unit and the uniformity of their physiological responses.

[1] Contribution No. 1011 from the Department of Botany of the University of Michigan.

At all events, the climax hypothesis rests upon the theory of limited succession. Although the replacement of one group of plants by another has been well-demonstrated in areas where man had destroyed the original cover, it is less well known to us under primeval conditions, about which our interpretation is largely circumstantial. Even more inference is needed to demonstrate convergence of several (or all) seres to a single climax.

The Kinds of Succession

The causes, the mechanics and the effects of vegetational changes are numerous and somewhat complex. Nevertheless, two main processes have been recognized generally (Tansley 1949), to which I venture to add a third one.

Autogenic succession is the displacement of one group of associated species by another group, primarily as the result of changes induced by the occupying vegetation itself. These changes affect *soil* (moderation of drainage, addition of organic matter, aeration or consolidation, turnover of buried elements), *microclimate* (attenuation or buffering of prevailing climatic extremes and fluctuations), and *vegetation* (increase of shade, of biomass and of stratification above and below ground).

Allogenic succession depends primarily upon changes in the physical environment itself, such as silting and erosion.

Biotic succession follows the interference of a living agent: a grazing animal, a parasite, a pest, etc. The chestnut blight, for instance has opened up the canopy of oak-chestnut stands, stimulating a temporary dominance in the intermediate layers of *Sassafras,* followed by a closing-up of the canopy by oaks. Likewise nomadic herds of buffaloes induced succession from tall to short grasses in the virgin prairie.

The Five Principal Stages

In the course of developing vegetation upon an originally unoccupied site, five main stages can be recognized.

A. *Pioneer stage.*—The physico-chemical nature of the raw parent material exerts a strong selection upon the flora, only a few very resistant members of which can tolerate these stressful conditions (high illumination, and evaporation, great compactness or looseness, low

water and nutrient content, maximum of meteorological impact and change).

B. *Consolidation stage.*—"Improvement" of the site allows vegetation to close and to stratify. Higher or more narrow requirements can be satisfied, greater use of the resources achieved. The stress is as much in the adjustment (through competition) of plants to one another as in their response to the physical environment.

C. *Subclimax stage.*—A highly developed vegetation on a somewhat differentiated and relatively rich (although rarely zonal) soil consists largely of species that cannot for long perpetuate themselves, as they are poorly adjusted to conditions of their own making.

D. *Quasiclimax stage.*—A somewhat imperfectly balanced vegetation, having essentially climax composition but on a slightly wetter or drier or steeper site, and with a generally immature soil still harbors many persistent subclimax species.

E. *Climax stage.*—The maximum of soil development (usually zonal) has occurred, and all spatially prominent species are fit to perpetuate themselves on an essentially unchanging site.

At each one of the stages, the vegetation exploits the environment in a different way, to a different extent, at a different level and is subjected to different stresses. Great tolerance and low requirements prevail in the pioneer stage; high requirements and low tolerance at the climax stage. Adjustment to physico-chemical adversities are necessary in the pioneer stage, capacity to utilize a rich environment efficiently is at a premium in the climax stage. Thus, *Oenothera* and *Danthonia* can grow on very permeable, dry, poor, exposed, sterile soils, but hardly outlive such conditions, whereas *Trillium grandiflora, Cornus alternifolia* do not make an appearance until the succession has proceeded almost to pure maple forest, but maintain themselves thereafter. In the intervening stages of the xerosere, many plants, such as *Solidago canadensis* and *Crataegus laurentiana* either cannot invade a pioneer community or do not develop very well within it and are in turn killed off by increasing shade and new competitors. Similar positions are shown for elements of the hydrosere.

Relays in Control

There are, then, as many thresholds as there are transitions between stages and, at each one of these, a *relay of controls:* the pioneer is under *edaphic* dominance, the consolidation and subclimax under *biological* and the climax under *climatic* controls. In other words the site as a whole shows a dominant response in A to parent-material; in B to soil; in C to vegetation structure; in D to minor topographic or edaphic features; and in E to climate.

Admitting that at all times the flora (the raw material of the plant cover) is controlled by the microenvironmental situation (microrelief, microclimate and other biotopic conditions), by the parent-material and the soil (*sensu stricto*), by the present topography (exposure, drainage, etc.) and by the climate itself, there is much observation to show that these various features of the landscape in many cases do not have *enduring power to limit.* It is in fact possible to consider the processes of succession as a series of *releases* from their control, more or less in the order given above. Thus, the goldenrods take over once the soil texture has lost its limiting power; the pines and hemlocks take over when soil-water has somewhat stabilized; maple takes over when shade has definitively set in.

One might consider these relays or shifts of ultimately controlling factors as veritable *unconformities* between the major stages. In fact, it almost seems necessary to recognize such a system of relays to account for the distinctness of plant communities. The *continuum* described and measured by Curtis and his associates (see Curtis and McIntosh 1950, Curtis and Brown 1952) does not seem to provide an ultimate argument against the discontinuity of floristic aggregates since it is plotted on a linear scale of values that are not necessarily linear themselves, and whose actually critical range is not known.

Obviously many plants—and entire communities—are able to outlive by far the conditions necessary to their original establishment, and this too is an important (and confusing ?) factor in the maintenance of distinct phytosociological units. For them to be displaced, a rather high threshold has to be crossed, a strong inhibition to be vanquished. This will be possible and immediate or relatively rapid under one soil-climate conjunction (*e.g.,* the St. Lawrence Lowlands) or else rather slow to almost static under another (*e.g.,* central Michigan).

Relative Importance of These Criteria

The debate on the nature and significance of climax centers upon three questions: the *internal dynamics* of vegetation, the *space* occupied by communities of presumably different dynamic status, and the *time scale* involved in vegetation change.

The *internal dynamics* concern the potential replacement of one species by another and of one whole community by another as a consequence of their uneven capacity for exploiting the environment which itself undergoes change (autogenic, allogenic and biotic). In this framework, groups of species stand with relation to one another in seres, all of which are theoretically convergent upon the climax. This has been described above.

The total *space occupied* in a region of uniform climate by the various plant communities of the A, B, C, D and E stages or types depends upon the relative area of long-undisturbed upland. Cliffs, dunes, inundated land and several other landforms are so slow in their geomorphic transformation as to indefinitely harbor A, B, and C vegetation only. Therefore, certain landscapes, even entire climatc regions will offer very little opportunity to E (or climax) vegetation as definable theoretically on the basis of internal dynamics.

One may ask: what is the usefulness of calling beech-maple forest climax in central Lower Michigan if it occurs only on exceptional topography whereas pines cover the landscape for miles? Of calling beech-maple climax in northern Ohio whereas broad expanses of floodplain elm-red maple-ash forest stretch over most of the area?

The *time scale* for an A — B — C — D — E complete succession may be a very long one. If climax vegetation is under the control of climate, how long must the same climate prevail in order to allow full development from A to E? There is no particular difficulty if, in terms of time:

$$(A + B + C + D) < E \quad \text{(ex.: s. New Zealand)}$$

But there are surely many cases where

$$(A + B + C + D) > E$$

and even

$$A > (B + C + D + E) \quad \text{ex.: Arctic regions)}$$

$$(A + B) < C > (D + E) \quad \text{(ex.: central Lower Michigan)}$$

and no doubt several other combinations. It must, of course, be remembered that a climatic shift which entails the replacement of one climax by another does not usually require a recapitulation of entire successions, but more

likely operates through the infiltration of communities by other communities of similar dynamic status (A by A and E by E).

It remains, therefore, that a simple application of the criterion of dynamic order in a well-definied A — B — C — D — E classification: a) is not always possible; b) is detectable only through a good deal of speculation; c) may have no descriptive value at all. In fact, what is the usefulnes of a climax-ordained scheme of vegetation where: a) the theoretical climax is only doubtfully established; b) it occupies very little total space; c) it is no more permanent than several other plant communities?

Regional Alignment of Controls

Whereas it may be true that, on a regional scale and within the duration of a climatic period, *climate* exerts the main control over vegetation, whereas *topography, soils* and available *flora* exert a secondary one, it is clearly possible for the latter three to *inhibit* succession and keep it more or less permanently short of climax status. In other words, entire areas are characterized by A, B, C or D types of vegetation and either lack true climatic climax stands (E) or have very little of them.

In Figure 1, the principal determinants of vegetation (1 to 5) have been plotted in terms of maximum, intermediate and minimum values (*a* to *e*). It is not assumed that the maximum (*a*) is necessarily the optimum in any sense as it may just as likely be an excess, nor that the minimum (*e*) is a pessimum, although this is more likely since it ordinarily registers a deficiency.

Categories 1 and 2 concern climate, and range from the equatorial to the frigid, and from the extremely wet to the very dry.[2] It should be pointed out, in passing, that climates differ just as much from one another in being *equable* (moderate, constant, showing least daily, monthly, yearly variation) or unequable as in being wet or dry, warm or cold. The warmest and wettest *1a2a* (Köppen's Af) is regarded as the most equable. As a rule all colder and/or drier climates are more "extreme," whence the sharper curves in *b, c, d* than in *a* position on Figure 1.

Categories 3 and 4 concern topography and soil, between which no *a priori* correlation is intended. Relief goes from the flattest to the steepest. Whereas in grading any one area climate can be referred to by using only one symbol in 1 and one in 2, with reference to topography even a general account of the landscape will require inclusion of two categories, such as *3b-3c* for Southeastern Michigan, *3d-3e* for the Yosemite area of the Sierra Nevada. In other words, the landforms that actually dominate over a substantial part of the area should be recorded. As for soil, drainage is the ultimate factor considered here, from the more or less permanently

[2] Rough equivalents in the Köppen system would be as follows 1a2a = Af; 1a2b, 1b2b = Am; 1a2c, 1b2c = Aw or As; 1c2a, 1c2b, 1c2c = Cf; 1d2a, 1d2b, 1d2c = Df (or maybe the latter Dw ?); 1e with any combination of 2 (a, b and c improbable!) = E; 1a, b, c or d with 2d = BS (maybe Cw or Cs with 1c) and the same with 2e = BW.

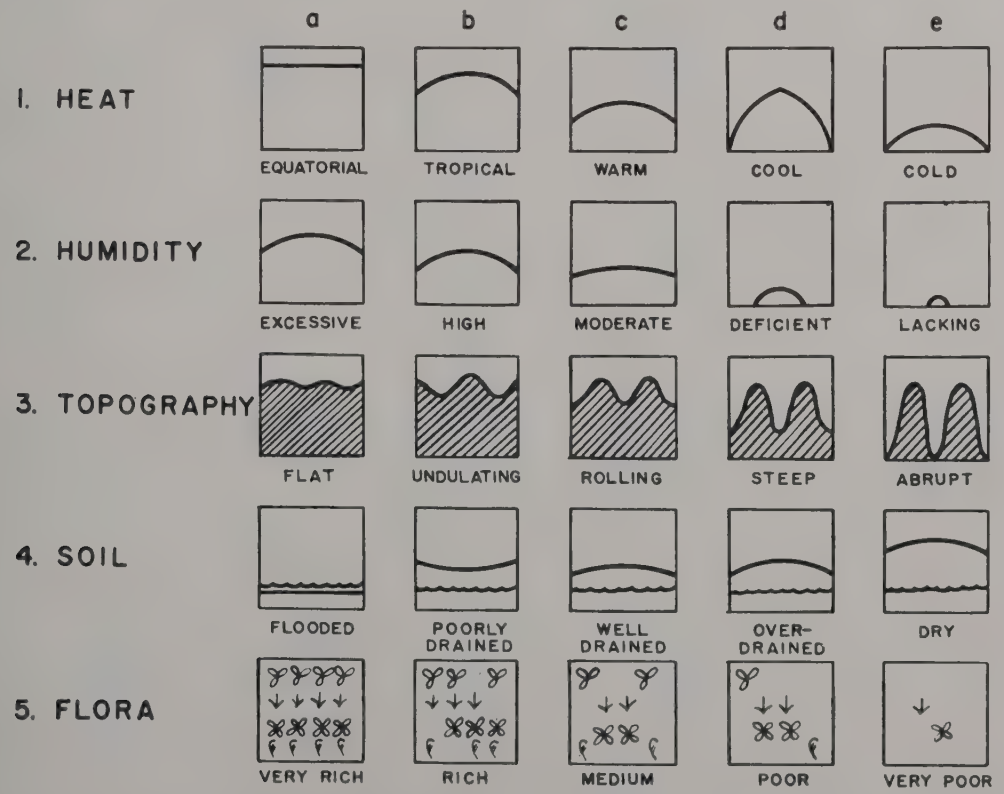

Fig. 1. A scheme for grading an area on its principal vegetation determinants. Five elements are considered (1 to 5) with five values from a maximum (a) to a minimum (e).

flooded (*a*) on a large scale (as in the Gran Chaco) to the very dry (*e*) as in the Sahara.

Category 5 applies to rich and poor floras, a relative scale where it is difficult to draw precise lines. The Lower Amazon probably has more than 25,000 species of vascular plants, and is therefore very rich (*a*), whereas many cool temperate areas of equal size have no more than 3000-4000 (medium or *c*) and Central Baffinland has only 100 (poor or *e*).

In Figure 2, sixteen areas in different parts of the world have been graded for the values defined above: the squares corresponding to the pattern of Figure 1 have been blacked out in each case to illustrate the situation in that particular area. For instance, in the upper left-hand corner, the diagram marked Montreal has a cool (1*d*) and moderately moist (2*c*) climate, a flat to undulating to rolling (3*a, b, c*) topography, a poorly to well-drained (4*b, c*) soil and a medium (5*c*) flora. The other fifteen diagrams of Figure 2 likewise conform to the design of Figure 1. As a result, four patterns emerge which show the *preponderance of a different ultimate control element* upon the regional vegetation as a whole.

Type A. Climatic control.—This is certainly a very widespread alignment in moist-temperate and moist-cold regions. Whereas the rate of succession is uneven, and occasionally quite slow, geologic differences in parent material are eventually overcome and a rather uniform association takes possession of all available upland.

Type B. Topographic control.—Where the landscape is *all* very flat or very steep, it is possible only to surmise what the internal dynamics of the vegetation would produce. The very species that might build up a climatic climax, although they may be within dispersal range, can hardly demonstrate their efficiency.

Type C. Edaphic control.—Permanently very wet or very dry (or very sterile ?) soils do not commonly extend as overwhelming regional features. Even so, they have only a temporary controlling force, unless the precipitation is weak, low, highly concentrated or very irregular.

Type D. Biological control.—Only where the precipitation and heat are both high and constant is the effect of climate overcome. Only under such conditions is the flora very rich. And although succession does take place, its ultimate result is not an association in the usual sense, but a broad community readily definable as to structure only and not as to composition. It would seem, here, that the hazards of dispersal and other historical factors are in full command.

In conclusion, it can be said that climate, topography, soil, and flora are all active factors everywhere but have the power to limit one another's influence on the ultimate development of vegetation. Conditions of high to moderately high rainfall associated with a not too-hot nor too-cold temperature always seems to provide the climate with great efficiency, *i.e.*, the capacity to overcome topo-

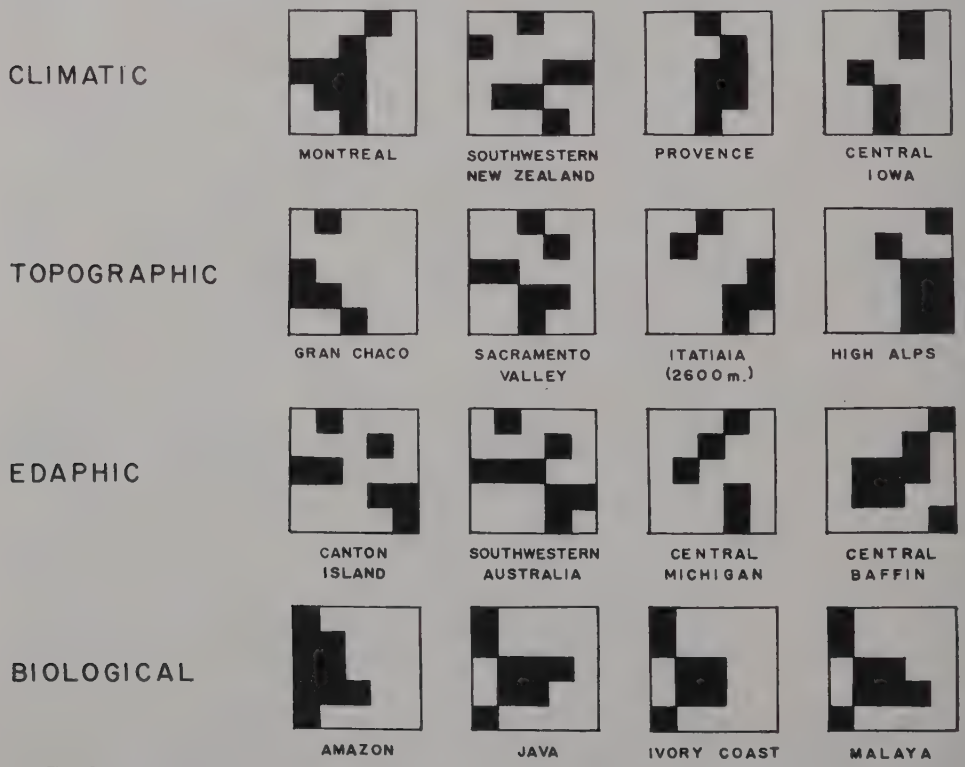

FIG. 2. An application of the grading pattern in Figure 1 to 16 different areas: the blacked-out squares correspond to equivalent values in Figure 1. The ultimate control of regional vegetation seems to be different in different areas, whether climatic, topographic, edaphic, or biological.

graphic and edaphic inhibitions. Some of the latter, however, are insuperable under any conditions.

References

Brown, R. T., and J. T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecological Monog. **22**: 217-234.

Cain, Stanley A. 1939. The climax and its complexities. Amer. Midl. Nat. **21**: 146-181.

Clements, F. E. 1936. Nature and structure of the climax. Jour. Ecology **24**: 253-284.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32**: 476-496.

Tansley, A. G. 1949. Introduction to plant ecology. George Allen and Unwin, Ltd., London. 260 p.

Pierre Dansereau

Department of Botany,
University of Michigan,
Ann Arbor, Michigan

PONTOPOREIA AFFINIS VAR. *BREVICORNIS* IN CAYUGA LAKE, N. Y.

Pontoporeia affinis Lindström, 1855 (Crustacea, Amphipoda) is one of the most significant profundal invertebrates of the Great Lakes and other deep oligotrophic lakes in North America and Europe. In the course of an investigation of the profundal benthic fauna of Cayuga Lake, New York, specimens of *Pontoporeia affinis* var. *brevicornis* were obtained that differ in certain respects from the described form. Samples of *Pontoporeia* were sent to Dr. Sven G. Segerstråle of the Zoological Museum, University of Helsinki in Finland, who, upon examining the specimens, noted these differences and recommended that certain changes be made known.

Pontoporeia hoyi and *P. filicornis* were described by Smith (1874) from material collected from some of the Great Lakes. The former species was found to be synonymous with *P. affinis* by Juday and Birge (1927) and *P. filicornis* was redescribed by Adamstone in 1928. In a revision of the genus (Segerstråle 1937) it was pointed out that *P. filicornis* was identical to the penultimate stage of the normal male of *P. affinis*. Segerstråle (1950) has suggested that *P. filicornis* may be a neotenic form of *P. affinis* and has termed it *P. affinis* var. *brevicornis* in distinction from the normal form which is referred to as *P. affinis* var. *typica*. Though *typica* has been found both in Europe and North America, including Cayuga Lake, *brevicornis* has been recorded only from North American lakes.

Mature males of *P. affinis* var. *typica* are recognized (aside from other characters not considered here) by the fact that the first antennae, which extend to near the posterior end of the body, have 31-57 segments in the flagella. The second antennae extend well beyond the posterior end of the body and the flagella have 42-72 segments. Mature males of *P. affinis* var. *brevicornis* are characterized by the reduction in the number and length of the flagellar segments and the consequent reduction in the length of the antennae. The described specimens had 14-19 segments in the flagella of the first antennae and 19-24 segments in the flagella of the second antennae. The second antennae extended to somewhat more than half of the body length.

The mature male *P. affinis* var. *brevicornis* found in Cayuga Lake differs from the above description. The flagella of the first antennae have 29-30 segments and the second antennae, which extend to about 60% of the body length, have 43-45 flagellar segments. In respect to segmentation the Cayuga form of *brevicornis* approaches the normal form. The concept of *Pontoporeia affinis* var. *brevicornis* should be broadened to comprehend those individuals with 14-30 and 19-45 segments in the flagella of the first and second antennae respectively, and with the second antennae attaining to as much as 60% of the body length.

It is urged that in future publications dealing with *Pontoporeia* some data on the antennal segmentation be included to contribute to our understanding of this animal.

References

Adamstone, F. B. 1928. Relict amphipods of the genus Pontoporeia. Trans. Amer. Micro. Soc. **47**: 366-371.

Juday, C., and E. A. Birge. 1927. Pontoporeia and Mysis in Wisconsin lakes. Ecology, **8**: 445-452.

Lindström, G. 1855. Bidrag till Kännedomen om Östersjöns Invertebrat-fauna. Kgl. Vet.-Ak. Förh. Årg. **12**.

Segerstråle, S. G. 1937. Studien über die Bodentierwelt in Südfinnländischen Küstengewässern III. Zur Morphologie und Biologie des Amphipoden Pontoporeia affinis, nebst einer Revision der Pontoporeia-Systematik. Soc. Sci. Fennica, Commentationes Biol., **7**(1): 5-183.

———. 1950. The amphipods on the coasts of Finland —some facts and problems. Soc. Sci. Fennica, Commentationes Biol., **10**(14): 1-28.

Smith, S. I. 1874. Crustacea of the fresh waters of the United States. Report U. S. Comm. of Fish and Fisheries, Part 2 for 1872-1873.

E. B. Henson

Department of Entomology and Limnology
Cornell University
Ithaca, New York

OBSERVATIONS ON FISH MORTALITY AND RIVER POLLUTION

This note presents observations relating to extensive mortality of eels (*Anguilla reinhardtii*) and sea mullet (*Mugil cephalus*) which occurred in the Upper Lane Cove River, Sydney, during a drought in 1951. The observations were made in a short stretch of brackish water situated just below a fresh-water weir near Fullers Bridge and about 1½ miles upstream from several factories which used to discharge effluent into the river.

Owing to lack of heavy rain since 1950, the overflow of fresh water from the wier became progressively less until by April, 1951, it was restricted to part of the small spillway at the southern end of the weir; the brackish water was beginning to emit an unpleasant odor (not of H_2S) and eels and mullet were beginning to congregate near the weir.

On April 19th, the concentration of eels in the water of the spillway was so great that these fish had arranged themselves not horizontally but more or less vertically, so that only a mass of heads was visible near the surface of the water: in approximately 100 square feet of water 3 feet deep in the spillway about 2,000 eels were estimated to be present, weighing about 4,000 pounds. Although this concentration rapidly decreased downstream, the 11 acre feet of water (at high tide) between the weir and Fullers Bridge were estimated to contain in the vicinity of 500,000 eels weighing about 1,000,000 pounds. The eels frequently protruded their heads from the water as though seeking air; they could easily be caught in a hand-net but then became very active and if transferred to the fresh water above the weir rapidly swam away. The mullet were excluded from the spillway itself by the sheer mass of eels, but they too were present in greatest concentration near the weir; their number between the weir and the bridge was estimated to be about 5,000,000 and their weight about 1,000,000 pounds. Considering both eels and mullet, therefore, the 11 acre feet of water between the weir and Fullers Bridge contained on April 19th approximately 5,500,000 fish weighing about 2,000,000 pounds (890 tons).

As the rainless period continued and the spillway became quite dry, the fish began to die frequently with bleeding and blackening of the gills. A few of the eels were observed to congregate near cracks in the wèir as though to immerse themselves in the fresh water trickling through. The brackish water was at first bluish black in color and emitted an offensive odor of pollution; then the water gradually clarified and the odor of H_2S became increasingly evident. By May 10th, virtually no living fish were to be seen. On May 20th, the drought was broken by heavy rains which caused the weir to overflow and flushed out the polluted brackish water tract of the river.

TABLE I. *Results of analyses‡ water sampled on 19th April, 1951*

Site	Salinity† gms. /liter	Nitrate microgms. /liter	Phosphate microgms. /liter		Sulphate	Sulphite	H_2S	O_2* p pm	pH
			Inorg.	Org.					
1.....	0.10	520	3	21	−	−	−	>5.0	7.8
2.....	5.69	284	121	33	+	−	−	n.d.	7.8
3.....	7.66	190	140	26	+	−	−	n.d.	7.8
4.....	11.39	12	171	59	+	−	−	<0.5	7.8
5.....	11.37	5	185	55	+	−	−	<0.5	7 8

‡Analyses carried out by R. S. Spencer, Fisheries Laboratory, C.S.I.R.O., Cronulla.
†Ocean salinity (Sydney Heads) 19.70.
*Dissolved O_2 content of O_2-saturated fresh water approx. 8 to 9 ppm.

Since the fish concentrations showed a close correlation with the amount of fresh water entering the brackish water, water analyses were carried out (Table I) on samples obtained on April 19th from the following sites:

Site 1. The fresh water above the weir at a point immediately above the spillway.

Site 2. The only slightly brackish water in the spillway.

Site 3. The slightly more brackish water below the weir at a distance of 10 feet from the spillway.

Site 4. The more brackish water half-way between the weir and Fullers Bridge.

Site 5. The stagnant water in one of the small brackish creeks on the eastern bank of the river between the weir and the bridge.

The most noteworthy features of these results are the figures for phosphate and dissolved O_2. Although the phosphate content of the freshwater from Site 1 is normal for this type of catchment area, the phosphate contents (especially inorganic) of the brackish water from Sites 2 to 5 are very high and are attributed to an input of phosphatic materials from the factories. The dissolved O_2 content of the fresh water from Site 1 is normal, but the extremely low values of less than 0.5 parts per million for the water samples from Sites 4 and 5 are well below the level necessary for fish life. Since a high phosphate content would not be expected to kill fish, it is most likely that the increasing concentration of fish from Fullers Bridge to the weir resulted from their endeavor to obtain O_2 from the fresh water entering the O_2-deficient brackish water below the weir. This lack of O_2 could have resulted from its utilization in the oxidation of H_2S which, although probably produced during the earlier stages of the pollution cycle, was not detectable until later when all of the O_2 had been used; this lack of O_2 rather than the presence of H_2S as such appears to have killed the fish.

The factory wastes which, in the past, discharged into the Upper Lane Cove River are known to have contained large quantities of sulphur-compounds and nucleo-proteins, from which H_2S and inorganic phosphate could be produced by natural putrefaction. Some of the substances in the effluent must have become absorbed by the river muds or fixed organically, since pollutions during dry periods have occurred at times when no factory effluent was entering the river. It is not known for certain what factors would have initiated the putrefactive changes, but it is known that the brackish water of the river was relatively stagnant and received little fresh water from the weir prior to the development of pollution. From the limited data available it would seem that several biochemical processes were involved in the pollution cycle; their complete elucidation would require more detailed study than has been possible during these observations.

A. B. COSTIN

SOIL CONSERVATION AUTHORITY,
KEW, E. 4,
VICTORIA, AUSTRALIA

ALGAE ON TURTLES: SOME ADDITIONAL CONSIDERATIONS

Certain algae grow epizoically on aquatic turtles. Edgren *et al.* (1953) recently discussed alga-turtle relationships, and provided a bibliography of pertinent papers. We wish to present a few more literature references, observations, and speculations.

Babcock (1938: 19) said of the common snapping turtle, *Chelydra s. serpentina,* in New England, "The carapace is often covered with an algal growth which gives it a greenish tint." W. H. Smith (1882: 657) stated, "Those (snapping turtles) found around Ann Arbor, Michigan, have a large number of fresh water algae growing upon their carapax." McCauley (1945: 139) said of the common musk turtle, *Sternotherus odoratus,* "When approached they are often difficult to see because of their resemblance to a knot on the stem (whereon they are basking). This illusion is usually furthered in specimens of all sizes by the luxuriant growth of algae upon the carapace." H. M. Smith (1950: 129) remarked of the alligator snapping turtle, *Macrochelys temmincki,* "For protection, this species relies chiefly upon camouflage. Dull-colored, mud-coated and with a growth of algae, these turtles easily conceal themselves . . ."

In Marion County, Florida, algae grow occasionally upon the Florida red-bellied terrapin, *Pseudemys nelsoni,* and very frequently upon the chicken turtle, *Deirochelys reticularia.* These two species may be added to the list of turtles known to be "attacked" by algae.

Allen and Neill (1950: 11) described the occurrence of algae on the alligator snapping turtle. They stated, ". . . in most specimens, large or small, that we have collected, the carapace is covered with a dense growth of filamentous algae." Edgren *et al.* (*op. cit.*) did not include this turtle among the species often "epizoöphytized." However, they examined only one carapace. Macrochelys bears algal growth about as frequently as any other turtle.

Allen and Neill continued, ". . . this algal growth always supports a copious crustacean fauna, including cladocerans, copepods, ostracods, and amphipods." Evidently Macrochelys may support a whole microcommunity of organisms. Apparently no one has investigated this aspect of the problem.

These authors further remarked (still with reference to Macrochelys), "A single smooth specimen . . . was taken in Bradford County (Florida); it was collected in a lake whose waters were apparently so dark as to inhibit the growth of algae." Turtles of the genera *Sternotherus, Kinosternon, Chelydra,* and *Pseudemys,* collected in clear spring runs of Central Florida, often support a growth of algae; while the same turtles, collected in nearby "black-water" streams or turbid lakes, are usually free of such growth.

At the Reptile Institute, various aquatic turtles are often kept in outdoor pens, and are supplied with pools of clear water. Under such conditions, almost any hard-shelled turtle becomes epizoized. We have thus observed algal growth to develop upon *Chelydra s. serpentina, C. s. osceola, Macrochelys temmincki, Sternotherus odoratus, S. c. carinatus, S. c. minor, Kinosternon b. bauri, K. b. palmarum, K. s. subrubrum, K. s. steindachneri, Graptemys barbouri, Chrysemys p. picta, Pseudemys f. floridana, P. f. peninsularis, P. f. suwanniensis, P. scripta troosti, P. nelsoni,* and *Deirochelys reticularia,* among United States turtles; and upon *Chelys fimbriata, Pseudemys decussata,* and *P. callirostris,* among exotic species.

We have also observed algal growth to develop on captive *Clemmys guttata.* According to Edgren *et al.,* this species is not epizoized in nature.

Sternotherus odoratus, S. carinatus minor, Kinosternon bauri, and *K. subrubrum* are among the Florida turtles most often epizoized in nature, but in captivity any of these may succumb to algal attack. If kept in clear water, the turtle becomes a veritable mass of algae in a few weeks' time. The plants grow, not only on the carapace, but also on the upper surfaces of the reptile's fore- and hindlimbs. In these areas the skin decays and falls away, exposing the underlying muscle. Death soon results. (Possibly, decay of the skin is produced by a fungus or other organism, secondarily invading tissues weakened by heavy algal growth.) Death from epizoization is probably very rare in nature.

Not only turtles but other aquatic reptiles may become epizoized in captivity. Among them are the American alligator, *Alligator mississipiensis;* the red-bellied mud snake, *Farancia a. abacura;* the red-bellied water snake, *Natrix e. erythrogaster;* and the diamond-backed water snake, *Natrix taxispilota rhombifera.* An epizoized alligator refuses to eat, and rapidly becomes emaciated; if left untreated it would probably die. Snakes apparently are not attacked by algae unless already in poor health. We have never seen algae on snakes in the wild, and very seldom on alligators.

Turtles of the genus *Pseudemys* often climb out of water onto a log or rock. Then they extend one or more limbs in odd fashion. The extended limb is held in the air, away from the substrate, the digits spread and the interdigital webbing stretched. Sometimes a turtle will rest on its plastron with all four limbs in the air. So far as we are aware, no one has offered an explanation of this behavior. Some herpetologists describe it as "sunning," but we have observed it to take place at night as well as by day. Furthermore, the flattened limb and foot are not held horizontally, to the skies, but vertically. Such actions may help to desiccate algae, fungi, and the like, plants which might otherwise gain a foothold on the turtle's skin.

Allen and Neill observed, "Two *Macrochelys* . . . were kept . . . in an outdoor aquarium, where they soon become covered with an unusually thick growth of filamentous green algae. This growth covered not only the carapace but most of the soft parts of the turtle as well. In spite of the density of the growth, however, the area about the nostrils and the region around each eye were completely bare of algae. Obviously it is of advantage to keep the eyes and nostrils free of algae; it is uncertain as to how this is accomplished. The turtles were never observed to claw at these areas, or to rub them against objects; such behavior, in any event, would scarcely explain the absolute lack of algae about the eyes and nostrils." The accompanying photograph (Fig. 1) shows an epizoized Macrochelys. Note the absence of algae about the eyes and nostrils.

Edgren *et al.* thought that the alga-turtle relationship was best defined as commensalism. They stated, "Camouflage for the turtle . . . would seem of little importance in view of the general absence of organisms predatory upon adult turtles," However, camouflage not only serves to conceal a creature from its enemies; it may

FIG. 1. Captive alligator snapping turtle, *Macrochelys temminckii,* with heavy growth of epizoic algae. The alga does not grow about the turtle's eyes and nostrils.

conceal a would-be predator from its prey. We have often watched foraging Sternotherus, Kinosternon, and Chelydra, both in aquaria and in the wild. These turtles often stalk small organisms very slowly and carefully. An epizoic growth probably helps to conceal the stalking turtle.

A turtle need not be covered with algae to be well camouflaged. A little epizoic growth along the seams of the carapace serves to break up the reptile's outlines, and suggests an inanimate object rather than a living creature.

Unlike other turtles, Macrochelys seldom forages actively. It feeds to a great extent upon fishes, which it lures into its open mouth by means of a wriggling, worm-like appendage on the tongue. Algal growth considerably enhances this turtle's resemblance to some natural feature of the stream or lake bottom. (See discussion of Macrochelys' feeding habits in Allen and Neill, *op. cit.*: 3-5.)

The feeding habits of turtles have received comparatively little attention from herpetologists. However, the available data suggest a correlation between feeding habits and the frequency of epizoization. The turtles frequently epizoized (Macrochelys, Chelydra, Sternotherus, Kinosternon, Deirochelys, and Emys) more often feed upon active prey, such as fishes, frogs, tadpoles, crayfishes, water insects, and the like. Among those infrequently or never epizoized, Pseudemys is largely herbivorous (or perhaps omnivorous in the case of *Pseudemys scripta*); Graptemys is to a considerable extent herbivorous and malacophagous, so far as is known; Chrysemys feeds mostly upon plants, worms, insect larvae, and snails; Clemmys is largely insectivorous, herbivorous, and scavenging (in the case of the two eastern species under consideration).

Thus, the turtles most frequently epizoized, are, in general, the ones that would most frequently profit from algal camouflage; *i.e.,* the ones that most often stalk active prey. The soft-shelled turtles, genus *Amyda,* constitute an exception; although carnivorous, they are not known to be epizoized.

Clear water, which normally would reveal stalking turtles, encourages the growth of camouflaging algae. Conversely, such growth is inhibited by dark or turbid water, in which turtles need little or no concealment.

Allen and Neill remarked of a captive Macrochelys, "Sometimes small fish such as *Gambusia* would nibble at the algae which covered the turtle's back, but the reptile never made a move at such times." Nevertheless, the turtle obviously watched the Gambusia, and snapped at them when they ventured near his jaws. In this instance the presence of algae attracted the fish, which

otherwise might have remained in some other portion of the tank.

We agree with Edgren *et al.* that few organisms prey upon adult turtles. However, the number of predatory species does not seem especially germane to the argument; what is important is the amount of predation, even though a single species of predator may be responsible for it. In the southeastern United States, large turtles are often preyed upon by the alligator. The smaller species are preyed upon rather frequently by the alligator, otter, and raccoon; and less frequently by the alligator snapping turtle, common snapping turtle, black bear, mink, largemouth bass and certain catfishes. The alga-turtle relationship may be a an ancient one; and not long ago (geologically), this country was inhabited by many large predators about whose habits we know little. Finally, man himself has been in the New World for 25,000 years or more, according to archaeologists, and has preyed heavily upon turtles during a large part of that time. Thus one cannot completely discount the notion that epicolous algae help (or have helped) to camouflage turtles from their enemies. No doubt concealment from potential prey is of much greater significance to the reptiles.

Edgren *et al.* noted that baby turtles were not epizoized, and stated, "There seems to be no clear explanation for this phenomenon; perhaps younger turtles shed the carapace laminae at a more rapid rate than older individuals." In general, baby turtles of aquatic species are more secretive than the adults; at least, this is true in the Georgia-Florida region where we have collected extensively. The young ones spend much of their time hidden in muck or beneath bottom debris. Usually they venture forth only at night, and doubtless forage over a relatively small area. The more frequent movements of adult turtles, and their wider activity range, probably increase the chances that they will encounter algal spores; and their frequent or occasional presence in open water during daylight hours may encourage algal growth.

Algae of the genus *Basicladia* grow only on turtles. Edgren *et al.* remarked, "What these algae gain from their turtle hosts is difficult to determine . . ." A few speculations may be offered. Any alga presumably would occupy all the substrata of a body of water, if it were able to do so. In other words, algal species are in competition with each other for substratum. Since very few species of algae grow on turtles, something about these reptiles must render them unsuitable for algal growth in general. Thus an alga that has become adapted to life on turtles has filled a niche where it is freed from most competition. Also, as a turtle moves from pond to pond, it may disseminate the epicolous alga. Much turtle movement takes place by night, and in damp places; thus the alga is not apt to desiccate. Even if the alga frequently desiccates, the method of dissemination yet supplements the production of spores. Although fishes, tadpoles, or other small aquatic herbivores may nibble at epizoic algae, they are not apt to devour the whole algal colony, for obvious reasons.

The alga-turtle relationship evidently varies according to the species of turtle involved. The presence of epizoic algae appears to be of great advantage to Macrochelys; at least useful to Chelydra, Kinosternon, Sternotherus, Deirochelys, and Emys; and of slight value to other turtles. The symbiosis is obligatory for certain algae of the genus *Basicladia,* according to Edgren *et al.;* it is not obligatory for any of the turtles, not even Macrochelys. In most cases the relationship appears to be one of mutualism, as defined by Allee *et al.* (1949: 245).

Summary

Certain algae grow epizoically on aquatic turtles. The alligator snapping turtle, *Macrochelys temmincki,* and the chicken turtle, *Deirochelys reticularia,* should be added to the list of species frequently epizoized. The Florida red-bellied terrapin, *Pseudemys nelsoni,* is occasionally "attacked" by algae. The algal growth on Macrochelys supports a crustacean fauna, about which little is known.

The clarity of the water is a factor affecting the density of epizoic algal growth.

Hard-shelled turtles of many species were held captive in outdoor pens and provided with clear water. They all became heavily epizoized. Turtles of the genera *Kinosternon* and *Sternotherus* succumbed apparently to algal growth which attacked the skin of the limbs; secondary invasion by a fungus or other organism is a possibility. Death from epizoization is probably very rare in nature.

In captivity, alligators and certain snakes may be attacked by algae. Such growth was never observed on wild snakes, and rarely on wild alligators.

Turtles of the genus *Pseudemys* air their limbs, perhaps to desiccate algae, fungi, or other epizoic plants.

A specimen of Macrochelys became heavily epizoized in captivity, but algae did not grow about the turtle's eyes and nostrils. It is not known how these areas are kept clear of algae.

Camouflage may serve to conceal a would-be predator from its prey. Certain aquatic turtles forage on the bottom of a lake or stream, and carefully stalk small organisms. These turtles are effectively concealed by algae on their shells. A turtle need not be covered with algae to be well comouflaged.

Unlike other turtles, Macrochelys seldom forages actively. Instead, it remains motionless on a stream or lake bottom, and lures fishes into its jaws. Algal growth is probably of great value to this species, whose very existence is dependent upon camouflage.

The turtles frequently epizoized feed to a considerable extent upon active prey. Those infrequently or never epizoized feed largely upon plants, carrion, or relatively inactive prey. However, the feeding habits of turtles are not well enough known to warrant insistence upon this generalization. The soft-shelled turtles constitute an exception to the putative rule.

In one case, fish were attracted by algae growing on the back of an alligator snapping turtle.

A growth of epizoic algae may occasionally help to conceal a turtle from some natural enemy. However, this aspect of the alga-turtle relationship does not appear to be very important. No doubt concealment from potential prey is of much greater significance to the reptiles.

The secretive habits of baby turtles may explain why they are not often epizoized.

Epizoic algae profit by their relationship with turtles. The obligate epicoles find freedom from the algal competition for substrata. Algae are carried from one body of water to another by outside agencies; turtles may provide an additional disseminating agent for the epicolous species. Colonies of epizoic algae are not likely to be completely devoured by aquatic herbivores.

The alga-turtle relationship varies according to the species of turtle involved. In most cases it appears to be one of mutualism, not commensalism.

References

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Philadelphia and London: Saunders.

Allen, E. R., and W. T. Neill. 1950. The alligator snapping turtle, *Macrochelys temminckii*, in Florida. Ross Allen's Reptile Inst., Spec. Pub. 4, Silver Springs, Fla.

Babcock, H. L. 1938. Field guide to New England turtles. N. E. Mus. Nat. Hist., Nat. Hist. Guides No. 2.

Edgren, R. A., M. K. Edgren, and L. H. Tiffany. 1953. Some North American turtles and their epizoöphytic algae. Ecology, **34**: 733-740.

McCauley, R. H. 1945. The reptiles of Maryland and the District of Columbia. Hagerstown, Md.

Smith, H. M. 1950. Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist., Misc. Pubs. 2.

Smith, W. H. 1882. Reptiles and amphibians of Ohio. Rept. Geol. Surv. Ohio, **4**: 630-734.

Wilfred T. Neill and E. Ross Allen
Research Division, Ross Allen Reptile Institute
Silver Springs, Florida

CAROLINA BAY LAKES: THE BOG MARGIN PROBLEM

In his recent paper, Frey (1954) has not only reversed himself in regard to the movement of the bog margin, which he formerly believed to be advancing into the lakes, but reverses his reversal when it comes to past time. The concept of present-day woody plant advance originated by Buell (1939) has been shown to be invalid (Wells and Boyce 1953) and it is difficult to imagine conditions which could make such an advance possible in an earlier period.

A brief history of these ideas pro and con may help to clarify the problem.

Buell (1939) in his argument for an advancing margin emphasized the shrub stolons and roots as growing outward into the water. He states: "The marginal encroachment is accomplished through the stoloniferous habit of some of the shrubs together with spreading superficial root systems of all the woody bog plants. A dense strong mat is thus formed which grows out into the water." Buell also mistakenly held that the "cypress trees with their buttressed bases and knees become nuclei for islands of shrubs and trees." He further writes: "In contrast to northern bog lakes, the most prominent difference of all is the pioneer role taken by aquatic trees in the advance of the vegetation into the lakes." Frey (1949) explained the present period advance as follows: "The fibrous peat along the protected northwest shore has probably resulted from the trunks, branches and leaves of vegetation growing near the shore and overhanging the water for distances up to 12 feet, falling into the water and sinking to the bottom. The relative amount of this deposit in a lake may well be an indication as to the rate of filling in, inasmuch as areal decrease is most important at the northwest end."

Wells and Boyce (1953a) in a paper given at the April meeting of the Southeastern Biological Association summarized the evidence against such an interpretation of the marginal data and later (1953b) presented seven important lines of evidence proving conclusively that no such marginal advance of the present shrub bogs is going on. On the other hand, these bogs are undergoing erosion under wave and current action with resultant enlargement of the lakes.

Frey (1954) reversing his former concept, adopts in part this correct interpretation in a paper entitled "Evidence for the recent enlargement of the "bay" lakes of North Carolina." However, Frey is unwilling to give up the marginal advance idea completely and holds it to have obtained in the past. In his summary he states: "The lake areas have been undergoing a modest phase of erosional expansion during at least the last 500 years. The author considers it likely that similar or even more extensive expansions, alternating with phases of filling and contraction, have occurred at various times in the ontogeny of these basins." In his discussion, he still adheres to the "cypress island" theory of Buell when he states: "Buell's (1939) concept concerning the role of pond cypress as the pioneer in the hydrosere of these lakes is probably correct and likewise the accumulation of "islands" of bay shrubs and organic soils around the bases of these trees."

In his attempt to hold to a marginal advance of woody plants into the lakes in the distant past, Frey at no point explains what environmental change has occurred which could induce a reversal of marginal movement.

We (Wells and Boyce 1953b) believe it can be shown that no such advance of a shrub or a swamp forest bog margin is possible at any time. Shrub-bounded bodies of water are frequent everywhere but they show no tendency to build peat laterally and take over the ponds. These shrubs are not mangroves and no mention of sphagnum (a marginal invader) is made by Buell or Frey. Frey's conception of the woody plants extending bogs laterally into the lakes after a period of erosional loss appears to be untenable.

References

Buell, M. F. 1939. Peat formation in the Carolina Bays. Bull. Torr. Bot. Club **66**: 483-487.

Frey, D. G. 1949. Morphometry and hydrography of some natural lakes of the North Carolina coastal plain: The bay lake as a morphometric type. Jour. Elisha Mitchell Sci. Soc. **65**: 1-37.

———. 1951. Pollen succession in the sediments of Singletary Lake, N. C. Ecology **32**: 518-533.

———. 1953. Regional aspects of late-glacial and post-glacial pollen succession of southeastern N. C. Ecological Monog. **23**: 289-313.

———. 1954. Evidence for the recent enlargement of the "bay lakes of North Carolina. Ecology **35**: 78-88.

Wells, B. W., and Boyce, S. G. 1953a. Advancing or retreating bog margins. Jour. Tenn. Acad. Sci. **28**: 190. (Abstract.)

———. 1953b. Carolina Bays: Additional data on their origin, age and history. Jour. Elisha Mitchell Sci. Soc. **69**: 119-141.

B. W. Wells and S. G. Boyce
Department of Botany,
North Carolina State College,
Raleigh, N. C.
and
Department of Botany,
Ohio University,
Athens, Ohio

REVIEWS

Principles of General Ecology[1]

Contents

In his preface Dr. Woodbury states, "The essence of ecology lies in its point of view. It approaches the study of the living organism from the standpoint of its relations to its environment. . . ." His book is organized and built around this theme. It is written as a college text for upper-division level and designed to fit a semester course. After a brief orientation section the book is broken into two main parts: the physical and the biotic environments. In each case a description of the environment precedes a consideration of biotic relationships. Early in the text the author states his position as an exponent of the ecosystem approach to an understanding of ecological phenomena. The ecosystem is later developed as the biotic community.

Twelve pages of the book are devoted to a consideration of historical perspective. Emphasis is placed on the sources of modern ecology starting from Buffon. Darwin, Pasteur and others who laid the foundations of modern biology are cited as well as such men as Lavoisier and Carnot who were important in the development of the ecological approach through their work on energy relations. Schimper, Merriam and Clements are recognized as three of the earliest of modern ecologists. By 1900 the young science of ecology had drawn from the allied fields of botany, zoology and geology, borrowed from mathematics and emerged with its own discipline. About 1925 the concept of biotic community originated and began its rapid development.

In seven chapters (125 pp.) the author covers the physical features of the environment and the requirements for the origin and maintenance of life. This treatment deals with the solar system and in particular the earth. The discussion includes a description of soils and their world distribution. The biota have developed adaptations ("an hereditary character which makes the possessor especially well fitted to meet some aspect of its environment") which meet the solid earth or soil conditions. Such structures as roots of plants and some of the locomotive devices of animals are considered in this respect. Fresh and ocean waters are discussed in terms of their physico-chemical and hydrodynamic properties. As in the case of soils, water is treated as a medium for life and aquatic adaptations of the biota are mentioned. The air and its constituents are the topics of a chapter which informs the reader of the nature of the substance. The nitrogen, carbon and oxygen cycle are included in this section. Adaptations of the biota are mainly responses to problems of gravity, respiration, evaporation and temperature as encountered in an aerial existence. Thus the reader learns of stiff stems in plants and skeletal support in animals which enable the organism to resist the pull of gravity. Problems of evaporation, respiration and temperature are solved by morphological, physiological and psychological adaptations.

From soil, water and air the text moves to a consideration of the origin and fate of radiant energy and its fundamental importance to life. The biotic adaptations to use or avoid radiant energy are mentioned under such topics as photosynthesis, leaf movements in plants and the photosensitive structures and behavior of animals. Skin pigmentation finds a place here and this leads to a consideration of temperature adaptations.

The movements of the earth in space are described in a chapter on gravity and periodicities. This is background to an understanding of such phenomena as the seasons and the distribution of radiant energy over the earth. Lunar rhythms and sun spots complete the discussion of extra-mundane phenomena which affect the terrestrial environment and biota. A following chapter on climate rounds out the treatment of the physical environment. After a general description of factors producing the earth's climate the author explains the origin of storms and their distribution. There is a section on climates over the geological time scale.

The physical environment defined, the author devotes a chapter (23 pp.) of his book to basic adaptations that meet this environment. He traces the level of organic control through ionic and osmotic regulation; the cell, thence to multicellular organization and division of labour. The physical limitations of organisms are discussed. A final adaptation of animals to the physical environment is epitomized as a "comfort quest." According to the author this is a behaviour which takes animals into comfortable situations, and which has to do with the struggle for ease or avoidance of pain. As an example, some animals of the desert avoid high temperatures by moving underground.

The remaining and largest part of the book is written under the heading of biotic interrelationships. Five chapters (77 pp.) of this section are devoted to the concept of biotic communities. Community organization is explained on the basis of a three way bondage amongst food producers, food consumers and habitat. A philosophy of community classification introduces the reader to various schemes of identifying and classifying biotic communities. Dr. Woodbury suggests the biocenose as a basic community unit which would parallel the species of plant and animal taxonomy. Higher ranks would be the biome (comprising a group of biocenoses), the biorealm (an aggregate of biomes) and finally the biosphere as the sum total of biota. Each designation except the last could be subdivided as the needs arise. As various biocenoses are recognized and described they might be named with binomials or trinomials as used in taxonomy. The first names would be capitalized and end in -ose. Biome designations would end in -ome, and those of biorealms in -alm.

Following community classification, two chapters inform the reader of the development of biotic communities and community analysis. The reader learns of the factors involved in plant succession as well as the various routes or seres by which the climax may be approached. Geological succession is briefly mentioned. The author next touches upon community analysis and outlines a plan of attack. The methods for community analysis are listed. These range from the description of a quadrat to the floatation method for detecting parasites. Advice is given on sampling methods and the use of sampling data.

In two chapters, the author deals with the complexities of plant and animal life in the biotic and physical environments. Energy input-output balance must be maintained within narrow tolerances if any organism is to survive. Factors influencing this energy balance lead to

[1] Woodbury, Angus M. 1954. Principles of General Ecology. viii + 503 pp., 167 figs., 5 tables. New York, Toronto: Blakiston Co., Inc. $6.00.

a consideration of the laws of the maximum and minimum. Conditions of space, food and shelter affect the welfare of plants and animals. Since these conditions are often in short supply, competition for them occurs. There follows a struggle for existence, the outcome of which may be measured by the valence (ability to meet variation) and vagility (power of dispersal) of a species.

In a separate chapter the author discusses the food relations of living organisms. This covers the nature of food materials and their importance in nutrition and growth. Adaptations for foraging are mentioned. Examples of food chains and the pyramid of numbers are used to tie food relations to the community concept.

Two chapters (29 pp.) deal with population problems and the adaptations of plants and animals that insure reproductive success. Population problems involve the interaction of the environment and population and factors capable of population control. The author makes a distinction between basic population which represents the breeding stock and annual population which represents basic population plus annual productivity. The elimination of most of the annual population produces a yearly cycle of numbers. There may be secular cycles which represent changes in basic population over a number of years. Possible explanations of such secular cycles are given. One of the basic causes of population behaviour is found in life history phenomena. As an example, an organism that breeds and dies in one year has a different population behaviour than one which lives several years and breeds annually.

Five chapters (92 pp.) take the reader into a discussion of evolution in the plant and animal kingdoms, migrations, biotic adaptations and the distribution of organisms over the earth. In a chapter dealing with migrations the author describes the conditions of day length and temperature that a migrating bird must meet depending upon the time and direction of migration. The causes and biological benefit of migration are discussed. Secular migrations are those which are not rhythmical or reversible. They are such sporadic movements as the seasonal swarming of grasshoppers or the exodus of snowy owls from the tundra. Under biotic adaptations the author considers the adaptations of organisms which meet the problems arising from contact with other members of the biota. Examples include: the feeding mechanism of the sundew, the gut tube of higher animals, pollination as effected by animals, mimicry, schooling, signal colours of birds and the characteristics of sex. In the last two chapters of the quintet Dr. Woodbury considers the historical and geographic distribution of organisms. The fossil record and Willis' theory of age and area are included in a discussion of centres of animal origin and routes of dispersal. The factors influencing animal distribution are discussed. Finally, a presentation of biotic realms and regions on land and sea summarizes the present day distribution of the biota.

The text ends with a quartet of chapters (68 pp.) which deal with plant and animal associations from simple mutualism to insect and human societies. The reader learns of commensalism, parasitism and predation. All terms are defined and examples are given from the plant and animal kingdoms. In a chapter on aggregations the author discusses the causes of animal grouping. In an association, animals are bound by no special organization although there may be some temporary order. Migrating flocks are an example of this. Societies, like the individual multicellular organism, are bound by complex internal forces. Two main lines of society development are traced in the animal kingdom. These lines culminate in the instinct bound ant and termite societies and human societies based upon a reflective intelligence. The final chapter of the book is an extension of this theme and a discussion of ecology and human affairs. The author points to the need of the ecological approach in engineering and in all activities concerned with the use of soil and water. Exhausted resources mean an exhausted nation. In his last pages Dr. Woodbury stresses the close bond between human populations and their environments. Human population cannot increase indefinitely, there must be checks. War, famine and pestilence are the result of tensions created by overpopulation. We can choose either these consequences of overpopulation or the solution for peace offered by an ecologist, "Birth control seems to offer the best chance for population control."

Critique

Within the past few years several books have been published which deal with the science of ecology. A recent and most successful work is that of Odum, which deals with specific fundamental relationships between organisms and their environment. To this reviewer Dr. Woodbury's approach is the antithesis of Odum's and, while ably demonstrating that life does not exist in a vacuum, fails to move from natural history and general biology to clear cut principles of ecology. On the other hand, the wide scope of the book makes it a storehouse of information and the approach does much for an ecological interpretation of natural phenomena.

The chapters on physical environment, particularly macroclimate and biotic communities, are commendable. The book is written in an easy to read manner with a minimum of ecological jargon. Terms that might cause confusion are defined. While a reviewer is bound to miss topics that seem to him important and feel that too much stress is placed on certain plant and animal groups, the bibliography of 24 pages is certainly broad enough to take the interested into most aspects of ecology. Moreover, the author speaks authoritatively of desert ecology in his home state. The plentiful illustrations, maps and photographs contribute a great deal to the book. In several maps, however (pp. 52, 146), reduction to page size has resulted in the loss of informative detail.

There are few errors worthy of mention. Since a tree of life diagram is used frequently in the text it is unfortunate that the illustration for the insect limb is a grotesque creature with four pairs of legs. One wrong theory perpetuated is comb cell size as the factor determining sex in the honey bee.

A deficiency in the text is the lack of any critical discussion of concepts which might stimulate the reader to independent thought. Moreover, throughout most of the book the author presents a great deal of factual material of an elementary nature. The text is designed for upper college level and presumably by this time the student has had or is taking a course in general botany and zoology. He will most certainly know that wings are an adaptation for flight and that some plants have a woolly or hair-like covering that reflects sunshine and reduces evaporation. Again, is is interesting to know the routes and weather conditions of migration but it would be more interesting to learn something of how animals navigate.

Doubtless as a result of the wide scope of the book many complex phenomena are covered in sweeping statements which may or may not be true. For example, "It is this remarkable adaptation of the internal skeleton to resist gravity that has made large size possible"; "This relationship (independent gametophyte generation, de-

pendent sporophyte generation) had to be reversed before independence from aquatic or moist habitats could be reached"; and "Birth control seems to offer the best chance for population control." The reviewer (at the time of writing) is still puzzling over this statement: "If an organism containing 20,000 homozygous pairs of genes should have a single mutation of one gene and it should be perpetuated, there would be possibilities of producing 2^{20} different combinations of this mutation with other genes."

Teachers who use this text will most certainly find it the source of many questions and perhaps fruitful discussion.

J. F. Bendell

Department of Biology
Queen's University
Kingston, Ontario

Adaptation in Micro-organisms[1]

This well-made and quickly published book presents fifteen varied papers, with a brilliant essay of introduction by Professor R. Y. Stanier. With each paper one may read a few closely edited and very stimulating pages of discussion among the participants of the symposium, a collection of the ablest representatives of the many American and European laboratories now at work in the field of the genetics of micro-organisms in the widest sense.

Stanier's brief and meaty essay is modest, but yet a model of its kind. He sets the stage by observing that the microbial environment is typically world-wide, measured not by geographical regions, but by the cubic millimeter, with hundreds of characteristic microflora concealed from the "gross ecological eye" in every gram of soil. The vast populations, the typically closed genetic systems and usual haploid existence, and the short generation times are matched to the short times during which any micro-environment can occur for exploitation by the organism. The dormancy powers of the typical microbe form the other side of its armor.

Stanier sets out to define and discuss the two types of adaptation, which he calls evolutionary, or adaptation to systematic environmental changes, and physiological, a response to fluctuating changes. This topic becomes one of the main issues of the symposium. Several papers are devoted to the distinction between the school of Hinshelwood, those who have bravely attempted to account for the enzymatic variability of micro-organisms by the principles of chemical kinetics, and the more orthodox after Delbruck and Luria, who have stressed the parallel between microbial enzymatic change and heritable change in higher forms. Spiegelman perhaps sums the matter up best by his clear statement that both the selection of mutant genic types and the induced synthesis of enzyme in response to an external inductor have been convincingly demonstrated. The clever replica plating scheme of Lederberg and the fluctuation tests of the first workers (Luria and Delbruck) do not leave much doubt that true mutations occur, though the British workers do not quite give up the field, in an understandable reaction to the fact that for some years their mechanism (induced enzymatic adaptation) was itself too little believed.

Ecologists will be pleased by a paper of L. F. Hewitt, who asks how it can be that unicellular, largely asexual, orgasims can still be found in a wild variety of strains, even among a single "species," when environmental range is small, sexual isolation meaningless, and natural selection ought to have produced a very few, robust forms to fill the appropriate niches. He argues that mere difference, not evident superiority of survival, seems to have been a basis for mutant selection. The attack of bacterial virus, with its notable specificity, fills the bill. The consequences of that attack are set forth in a neat review, stressing the mutual control by phage of bacterial evolution, and by bacteria of phage evolution. He touches upon, but cannot exhaust, the wonderfully complete spectrum of "forms" extending from the bacterial transforming factors through lysogenic phages to genuinely virulent virus strains. This field is explosively growing, but a neat general background for its study is found here.

Perhaps the most exciting topic of the symposium is set forth in a group of four more or less connected papers, by Spiegelman and Halvorson from the U.S.A. and by the Paris School, reporting work by M. Cohn, Monod, M. R. Pollock, and Slonimski. The problem attacked is one of the most fundamental to understanding of the cell: the mechanism of formation of specific proteins (enzymes are the actual examples under study). It is known that labelled cells produce newly induced enzymes (i.e., not invariably present) out of the unlabelled medium, and not out of pre-existing protein. This frees the process of induction from reduction to effects of a specific pre-existing precursor, and allows the bold hypothesis that the induction mechanism is the general mode of protein synthesis. That inducers may be unmetabolized materials, or short-lived like free penicillin which can yet induce penicillinase formation for an indefinite time, makes it plain that the inducer does not simply combine to complete a pre-formed enzyme. On the other hand, it becomes possible to claim that every necessary enzyme is "induced" by the normal products of intermediate metabolism. The existence of cycles of coupled enzyme reactions supplying their own "inducers" as their end products becomes a realistic, far from demonstrated, logical substrate for the familiar concepts of "self-reproducing" particle. Thus a whole hierarchy of biochemical schemes might be found out one day, extending from the familiar ones of nutrient metabolism through enzyme adaptation to the permanent and discontinuous mutations themselves. Pollock even suggests the "possibility of directed heritable mutations" produced by environmental factors, while he does not fail to point out that the self-stabilized feedback nature of the cycles might explain why we have not seen many such changes demonstrated.

It is most significant that the models here discussed by these ingenious biochemists still require somewhere the storage of a coded pattern related to the shape of the substrate molecule. For it is typical that the same substance, indeed, the enzyme's substrate itself, may serve as an inducer in a cell which can acquire the ability of enzyme production, and yet inhibit specifically and nearly completely, but only for a time, the enzyme's formation when the cell tested already has the ability. This paradox of Monod's he ascribes quite believably, but admittedly only tentatively so far, to the competition between exter-

[1] Gale, E. P., and R. Davies (editors) 1953. Adaptations in Micro-organisms. Third Symposium of the Society for General Microbiology. viii + 339 pp. Illus. + plates. New York: Cambridge University Press. $6.00.

nal and internal inducing compound. Now, he concludes that the inhibition could never be complete if the added compound merely formed a part of the "organizer" which is assumed to make the enzyme form the amino-acids. It must act rather in a metabolic chain to form only a precursor of some portion of the "organizer." Then it could inhibit by competition, and find the inhibition removed because it has itself provided material for the eventual formation of more of the active substance. There must be, then, some specific pattern, prior to the enzyme itself, which "recognizes" the features of the substrate. So we are back to the recording tape of the DNA, perhaps according to the Watson-Krick model. Again the static picture of the gene and the dynamic whirl of the biochemist find their complementary importance, mirrored perhaps in the rapid metabolism of the cell in its right micro-niche with its resistant, inert dormancy in other states. This is a domain, one may hope, for investigation for some time to come, but not for the too familiar indecencies of political controversy.

There is no substitute for the detailed study of the papers of these authors. Even the biologist who has nothing to do with cells and enzymes ought to look a little at least at the summaries, the diagrams, and the discussion, for is there not here the first hint for a long time of how the wonderful plasticity of the cell of the embryo can be explained? Development and genetics are on the edge of unification in the study of the very cells whose solitary life makes them seem undeveloping.

Other papers of the volume include a pair on the nature of adaptation, whether mutation or not (Hinshelwood and Dean, Ravin); a pair on temperature adaptations in various micro-organisms (Clegg and Jacobs, Knox); three on drug resistance (Abraham, Barber, Mitchison); and two on other than bacterial forms, one on adaptations in *Paramecium* by Beale, and one on fungi by Brown and wood. The whole volume is an invaluable one, and like the Cold Spring Harbor Symposia, should attract an audience far beyond the specialists who sponsor it. Dr. Pirie adds a comment, in his acid way, that the "Symposium has produced a rich crop of metaphysics." I think he means *speculation;* he is right in that, but has failed to make quite clear whether it is a word of condemnation or of praise. For the present reviewer it is praiseworthy, and if not truth itself, then its precursor, or better yet its inducer.

P. Morrison

Department of Physics
Cornell University

A First Book of Ecology[1]

Here is an important book to be highly recommended to the general reader for the clear and interesting way it explains the relation of plants and animals to their physical surroundings, to each other and to man. The main idea of the book is stated in the title, *The Web of Life,* which the author explains to mean that every plant and animal influences the survival and, in turn, is influenced by the survival of other plants and animals. Of course, this needs no explanation to an ecologist but Mr. Storer uses it as a most effective and convincing approach for the layman or even the general student of biology. *The Web of Life* is being called "a first book of ecology" which is a title well deserved for the directness with which it tells what ecology is about and how it is important to man.

The author develops this theme in a forceful narrative style describing the nature of forest and grassland communities. First, he presents the basic conditions of soil, water and climate upon which plants and animals depend. Then, he explains the extent to which the existence of plants and animals modify the prevailing conditions and the increasingly complex relationships which develop between them in respect to shelter, food supply and reproduction. Finally, he shows how this succession of physical and biotic changes results in the establishment of relatively permanent (climax) communities of plants and animals in harmony with the geographic and climatic conditions. In this connection he discusses the significance of limiting factors, adaptation, seasonal changes and cyclic regulation of numbers in contributing to the balance of nature. In a stirring account of the remarkable life cycle of the Pacific salmon he presents another fine example of the nature and significance of such relationships. Throughout the book he stresses the importance of recognizing and maintaining the balance of nature as the only sound basis for all work in the conservation of the natural resources of soil, water and wildlife and the vital importance of this to the welfare of man.

As pointed out in the introduction by Fairfield Osborn, John H. Storer is unusually well qualified by years of experience to write a book of this kind and to judge wisely the importance of its facts and message. Graduated from Harvard, he spent twenty-five years as a farmer and in 1927 won the gold medal of the Massachusetts Department of Agriculture for contributions in poultry breeding. Since 1937 he has been naturalist, wildlife photographer, lecturer and author. He has prepared sound-track films for the Conservation Foundation of New York on the principles of ecology and conservation. He pioneered in the slow-motion photography of the flight of birds and for four years has been president of the Florida Audubon Society. Compared to other books of its kind, such as Osborn's *Our Plundered Planet* and Vogt's *The Road to Survival, The Web of Life* is not so extreme in its position and may well make a more favorable and lasting impression upon its readers.

A center section of the book contains 44 plates of photographs obtained from the National Park Service, National Audubon Society, United States Forest Service and the Soil Conservation Service. These are excellent pictures which high-light the text and effectively tell the story in their own right.

William A. Dreyer

Zoology Department
University of Cincinnati

[1] Storer, John H. 1933. The Web of Life. xii + 144 pp., 44 plates. New York, The Devin-Adair Company. $3.00.

Plague—An Ancient and Persisting Ecological Problem[1]

During an intensive wartime study of the literature of epidemiology the reviewer could find no more useful discourse on the epidemiology of insect-borne disease than that contained in two venerable but little-known papers by L. Fabian Hirst in the *Ceylon Jurnal of Science*. Now, 27 years after publishing these papers, Hirst has put together an up-to-date story of plague which cannot fail to fascinate anyone with the slightest interest in ecological problems. The reviewer literally found it difficult to set this volume aside and he will testify that recent books have seldom had this effect on him.

Epidemiology is a branch of ecology but rarely does one read the works of an epidemiologist who recognizes this fact and who thinks along ecological lines. Also, there are very few specific ecological problems which have received two thousand years of investigation conducted and recorded by a succession of the ablest students and writers of their times. Hence, the author, who set out to present "a study of the development of human beliefs about the origin of the malady from the era of primitive man to the present day," has presented us with a unique case history of the development of ecological thought. It is very instructive to follow the meandering trail up to the author's statement (on p. 422): "Man himself, a vegetable microorganism, a cold-blooded arthropod vector, and its warm-blooded rodent host all share in the genesis of epidemics of plague. The ecological relationships between these four components are not only of great complexity but vary enormously in different countries and even in different parts of the same country."

The story of plague emerging from centuries of study is that of an enzootic which may smoulder for long periods in the "campestral" (= "sylvatic") from among wild rodents of the great plains regions of all continents. The ectoparasites of these rodents are inefficient vectors and human outbreaks from this source apparently exhibit an unexplained tendency to be of the pneumonic type. Pneumonic plague outbreaks tend to be self-limiting, possibly because increasing virulence decreases the probability that a victim will survive long enough to spread the infection. Three times in recorded history plague has broken from its usual confines and, in the bubonic form, become the "Plague of Justinian," the "Black Death," and the "modern pandemic" which started from Hong Kong in 1894 and (perhaps) ended about 1940. All major human outbreaks can apparently be regarded as preludes or after-shocks of these three great upheavals.

[1] Hirst, L. Fabian. 1953. The conquest of plague. A study of the evolution of epidemiology. xvi + 478 pp., 16 figs., 6 plates, 3 maps. Oxford: Clarendon Press. $11.00.

The biological event initiating a potential pandemic is simply the introduction of plague, by flea transfer or other means, into a *Rattus* population of adequate density which is supporting an adequately dense population of appropriate fleas. Various flea species can support an enzootic but "no epidemic of human plague nor rat epizootic of any magnitude has ever occurred anywhere during the course of the recent pandemic in the absence of an adequate density of *Xenopsylla cheopis*" (p. 302). Even an epizootic, such as one which continued for 10 years in Seattle but gave rise to only three human cases, may be of slight public health importance if contact between man and rats is restricted. Here the ecological relationships are subtle. In Europe, fleas from *R. rattus* have been most successful in biting man but in parts of Bombay local conditions have made *R. norvegicus* the greater hazard. The virtual immunity of Europe during the recent pandemic can be ascribed to some very interesting events occurring in the world of rats.

There is no occasion for the reviewed to attempt a further summary of Hirst's thesis. This is a fascinating ecological study of a problem of great general interest, hence it is an excellent volume through which to introduce the skeptical layman to ecological thought. Here he will find incontestable evidence that it is worthwhile to study taxonomy, even to separate very similar species (fleas in this case) on the basis of trivial morphological characters. Here also he should become convinced of the great potential value of purely academic studies aimed at discovering the effects of climatic factors on breeding rates, longevity, habits, or, in fact, just about any feature of a population which an ecologist may propose to study. This historical approach is vivid and convincing and, if we can learn from history, all modern ecologists might ponder some of the pitfalls recorded in this case history. The reviewer was struck by the parallel between the modern fad for "group" or "team" research and the numerous national and international commissions investigating plague in India. Of these Hirst justifiably reports (p. 133): "The really illuminating observations however, were made by individuals working independently, often with inadequate facilities. Group mentality, as usual, proved singularly barren of new ideas."

From the size of this book, and the quality of paper and binding, one can only conclude that it appears to be terribly overpriced. Probably it would not be a "best-seller" anyway but the reviewer anticipates a regrettably small audience for this very readable and valuable book.

LaMont C. Cole

Department of Zoology
Cornell University

A New Textbook of Geology[1]

The publication of a new textbook in a field related to one's interests is always an event. An occasion to refresh one's understanding of general phenomena and principles, a cause for new questions. It may be somewhat reassuring that the book does not contain too much that is new, that one's grasp of the subject is still fairly good. It is irritating, however, to encounter the same stereotypes, the mirror images of time-worn engravings and the repetition of well-tested pedagogical tricks. How welcome is a really new text, with something more than "recent advances" or an encyclopedic coverage of the subject, with a genuinely fresh perspective and an original treatment.

The present "Geology" by von Engeln and Caster is certainly deserving in this respect. It is clearly written, abundantly illustrated with photographs and diagrams, interspersed with very readable tables, and well organized.

There are four principal parts.

The first is an introduction to the elementary facts

[1] Von Engeln, O. D., and K. E. Caster. 1952. Geology. xii + 730 pp., 373 Figs. New York, Toronto, London: McGraw Hill. $7.50.

concerning the "materials of the earth." This can be well understood even by students who know little chemistry. There follows an account of the history of early (and fundamental) geologic ideas. Some effort is made, here, to present the development of the earth sciences in their social and historical context. But the relevance does not always emerge clearly. For instance, when the principle of stratigraphic succession (established by Werner, von Schlotheim and William Smith) is described, the following statement is made (p. 20): "Because the life spans of these three men center upon the Revolutionary period of American history, 1776 is suggested as the birth year of both the American nation and modern geology." Easy to remember, of course.

The second part relates "the natural history of igneous rocks." It examines successively the origin and composion of magma, the phenomena of intrusion and extrusion, vulcanism, the kinds of igneous rocks and their weathering. The photographs brilliantly show the typical cast of igneous rocks and the landscapes they dominate, the surge of volcanoes, the deposits of ash and the subsequent moulding by weather. The diagrams of Dave Miller and Anneliese Caster are vividly drawn. The texture of individual materials is rendered very real in photographs such as that of the "bag of nails" (Fig 26) or the "ropy lava" (Fig. 34). Even more interesting is the amorphous substance of volcanic tuff which is illustrated by a Toltec idol (Fig. 24), or the hard, polished porphyry, represented by a Roman carving (Fig. 36).

The third part deals with "structure, process, form." This dynamic review of geomorphology starts with an explanation of sedimentation and a classification of sedimentary rocks, the role of underground water is given a whole chapter, where perched water tables and geysers, for instance, are explained and well illustrated by Anneliese Caster and Mary Guerrière's drawings. Although most of the photographs are taken in the United States, many of them are from other areas, and not only when the point to be made does not have an American counterpart. The chapter on diastrophism culminates with a famous and dramatic photograph of the San Francisco earthquake (and fire!). This is followed by a detailing of tectonic phenomena and metamorphism. This part closes with seven chapters on the sculpture and modelling of the land under the most contrasting climatic conditions: in mountains, in the sea, in humid, arid, and glacial regions.

The fourth part naturally continues this last chapter, since the authors have chosen to relate their geologic history backwards. It may be no particular hardship for some biologists to read evolution backwards. It is true enough that we extrapolate our knowledge of the living and the recently fossilized into our interpretation of older forms. Those of us who are addicted to a less practical but more logical method may be a little embarrassed. But this may be a mere esthetic quibble. The geologist, as he looks at a landscape, does uncover the older records by lifting the more recent debris and, step by step, goes back in time, and in depth! This adventure unfolds itself in the 331 pages that detail geologic history. This part too is abundantly illustrated. A series of maps runs through the text and shows the shifts in continental emergence and marine transgression from period to period. The photographic illustrations and the drawings of characteristic organisms are very well done.

One may regret here, as in the other parts of the book, that controversial issues and indeed any discussion of points of view or hypotheses seem to be avoided. Not that the authors give the impression that the "truth" is known, for they do present alternative explanations, but they do not raise any issues. For instance, continental drift is mentioned twice (but not the name of Wegener!) but is not posed as a problem. (This is the more surprising since one of the authors has played a leading role in discussions on this topic.) In fact, the whole book tries much more to achieve an effect of exciting revelation of fact than of intellectual awakening to the problems of earth science.

It seems to be the authors' purpose not to aim too high and to make their statements at a very concrete level. This is not a book of ideas on geology; essentially is is a book of facts about the earth. Maybe one should not quarrel with this, and trust that students will derive "inspiration" from such a contemplation. But could not ideas have been stressed a little more?

In this same connection, it seems to be unfortunate that all formal definitions have been avoided, to be replaced by a diffuse "explanation" of the word in the text where it is first used. I am aware that this has been done in many textbooks and is approved by many educators. I doubt whether it generates clear thinking or a proper weighting of words. It is certainly in harmony with the pragmatic approach that high schools develop in their students and thus provides no intellectual shock which would deter freshmen and sophomores from the study of geology.

In fact, I wish von Engeln and Caster had written a more highbrow textbook because I know they have more opinions to state and issues to raise than they do here and because I am convinced that would be as good for the students at it would be for us ecologists who turn to them for a summary of current thinking on geological processes and the history of the earth! As it is, there is still a great deal that we can obtain from this big book: checks on our knowledge of particular situations, concise but rigourous outlines of geological successions and ready bibliographic references. The latter, at the end of each chapter, are briefly annotated. The authors do not fail to point out whether the said reference is "in simple language" or "specialized." There are, of course, *no titles in other languages!*

In spite of these reservations (maybe directed against a cultural current rather than against these writers?) one can only have respect for the exquisite workmanship of the authors and illustrators who have put together a very comprehensive text, very well balanced and have made every page alive.

Pierre Dansereau

University of Michigan

North American Prairie[1]

Dr. J. E. Weaver, Professor Emeritus of Plant Ecology, University of Nebraska, has just written the "Book of Knowledge" about our prairies. It is called "North American Prairie." Many books about plants have been slanted for the scientist, and others have been written for laymen. This one will appeal widely to both groups because it is firmly based on scientific investigation but is written in Weaver's clearly readable style which can easily be understood by anyone interested in nature.

This book climaxes Weaver's long career of teaching, researching and writing. It reveals the skill of the master scientist.

The author covers his theme admirably in one line from the preface, which reads as follows: "The prairie has been thoroughly examined as to its way of life both above ground and deep into the soil, which it efficiently protects." There are 16 chapters each pyramiding fact upon fact coherently throughout.

A comprehensive list of grasses, forbs and shrubs that populate the prairie is described. About 200 photographs and drawings, which are themselves works of scientific art, show the plants in their natural habitats, giving further reality to the text.

The virgin prairie is described, and vivid discussions about its settlement, degeneration due to plowing, grazing, fire and drought, plus its recovery after rest, are included. A dramatic, vigorous lesson about the conservation of natural resources is given. If the knowledge about practical land management portrayed were put to use by the land-owning public, a large part of the problems arising from mismanaged land would be wiped out.

Weaver concludes this fine book in a reflective mood with this eloquent quote with its meaningful theme, "Grassland soils through untold centuries have been thoroughly protected by the unbroken mantle of prairie vegetation. The vegetation and soil are closely related, intimately mixed, and highly interdependent upon each other and upon climate. Hence prairie is much more than land covered with grass. It is a slowly evolved, highly complex organic entity, centuries old. It approaches the eternal. Once destroyed, it can never be replaced by man."

B. W. Allred
Soil Conservation Service
U. S. Department of Agriculture

[1] Weaver, J. E. 1954. The North American Prairie. xi + 348 pp., 87 fig. Lincoln, Nebr.: Johnson Publishing Co. $5.00.

ANNOUNCEMENT

A preliminary meeting was held recently to explore the possibility or advisability of developing a uniform system for use in coding biological taxonomic entities. Participants at this exploratory meeting were from the Library of Congress, the United States Department of Agriculture, the Smithsonian Institution, and the Chemical-Biological Coordination Center of the National Research Council.

It is known that several laboratories are entering the results of their experiments on machine or hand-sort punch cards and that at least a few are listing the species of plants or animals tested by means of a code on these punch cards. In order to facilitate the exchange of information between various laboratories, it would seem to be highly desirable for these research groups to use a uniform taxonomy coding system. If the need or usefulness of uniformity is confirmed by sufficient biologists, a start on the formation of a standardized code should be made as soon as possible so that the conversion from individual codes can be accomplished with a minimum of effort.

The interested persons who have been informally discussing the project do not want to set plans in motion for the actual codification unless there is a real or potential need for it. Our immediate problem, therefore, is to determine what areas of biology could be usefully served by a standard taxonomic code. We are, therefore, requesting that those who have worked out or adopted a system for coding taxonomic entities, or who may be conducting work which might benefit from such codification, submit their opinions concerning a standardized biological taxonomy code.

Letters should be addressed to:

Dr. G. Congdon Wood
Chemical-Biological Coordination Center
National Research Council
2101 Constitution Avenue, N.W.
Washington 25, D. C.

INDEX TO ECOLOGY, VOLUME 35, 1954

A

Abies balsamea, balsam fir, recurrence of spruce budworm infestations in, 62
Adaptation in micro-organisms, reviewed, 587-588
Agar, W. E., reviewed, 99-100
Agar's individual organism, review, 99-100
Aggregations, animal, equations describing, 361
Alabama, southern, forage production on longleaf pine lands of, 59
Alberta, prairie region of, bees and pollination of alfalfa in, 453
Alfalfa, pollination of, and bees, 453
Algae, nitrogen and phosphorus in cells of, 348
Algae on turtles: some additional considerations, note, 581-584
Allen, E. Ross, co-author, note, 581-584
Alligator Harbor, Florida, factors controlling distribution of oysters in, 322
Allred, B. W., review, 591
Analysis of mixed grass range vegetation, methods in, 431
Analysis of the spruce-fir community on the Kaibab Plateau, Arizona, article, 316-322
Animal ecology, reviewed, 301
Another speculation on reality, review, 424-425
Anthony, Margery, article, 334-347
Appalachian forest types, plotless sampling trials in, 237
Arctic lake, mortality of whitefish in, 388
Ardea herodias treganzai, great blue heron, temperature regulation in young of, 466
Arizona, an anlysis of the spruce-fir community on the Kaibab Plateau, 316
Arthropods of the tree-hole complex, 208
Atwood Lake, Ohio, hydrobiology of, 305
Auerbach, Stanley, co-author, article, 208-222
Australia, eastern, soil phosphate and delimitation of plant communities in, 370
Australia, Macquarie Island, an example of long distance dispersal, 569
Australia, observations on fish mortality and river pollution, 580
Australia, soil mantle movement in relation to forest clearing in southeastern Queensland, 380

B

Balsam fir, recurrent infestations of spruce budworm in, 62
Barnes, Betty Martin, and Robert D. Barnes, article, 25-35
Barnes, Robert D., co-author, article, 25-35
Bartholomew, George A., Jr., and William R. Dawson, articles, 181-187, 466-472
Bay lakes, Carolina: the bog margin problem, 584
Bay lakes, North Carolina, evidence for the recent enlargement of, 78
Beach seine samples, variations in, 18
Beadle, N. C. W., article, 370-375
Beer, James R., Paul Lukens, and David Olson, article, 437-445
Bees, ecology of, 453
Bendell, J. F., author, review, 585-587
Berkeley, California, influence of pine shade and litter on evaporation from soil at, 397
Berner, Lewis, and William C. Sloan, note, 98
Big Bend region of Texas, ecology of Opuntiae in, 334
Biotic communities, flood plain, of lower Mississippi valley, 126
Blais, J. R., article, 62-71
Bluegill population, food turnover of, 490
Body temperature and water requirements in the mourning dove, *Zenaidura macroura marginella*, article, 181-187
Bog margin problem, Carolina bay lakes, 78, 584
Bogs, pollen study of two, in Texas, 462
Bond, T. E., co-author, note, 562-569
Bottomland hardwood species, effects of saturated soil on seedling growth of, 36
Boyce, S. G., co-author, note, 584
Bradley, J. S., co-author, reviewed, 423
Brasington, J. J., co-author, article, 59-62
Breder, C. M., Jr., article, 361-370
Brink, V. C., note, 94-95
British Columbia, survival of plants under flood in, 94
Brown, W. L., Jr., note, 421
Bruner, W. E., co-author, article, 117-126

C

Cacti, ecology of, 334
California, Berkeley, influence of pine litter and shade on soil evaporation at, 397
California, factors affecting plant growth on serpentine soils, 259
California, plant species in relation to serpentine soils, 267
Callibaetis floridanus, mayfly nymph, in brackish water, 98
Campbell, Robert S., co-author, article, 59-62
Canada, Ontario, ecological studies of forest trees at Chalk River, 406
Cannon, W. A., note, 293-295
Carex kobomugi at Island Beach, New Jersey, note, 289-291
Carolina bay lakes, enlargement of, 78, 584
Caster, K. E., co-author, reviewed, 589-590
Cattail die-off, experiment to prevent, 418
Cayuga Lake, N. Y., *Pontoporeia* sp. from, 579
Cell contents of nitrogen and phosphorus as a measure of their availability for growth of *Microcystis aeruginosa*, article, 348-353
Chalk River, Ontario, ecological studies of forest trees at, 406
Chandler, D. C., review, 300-301
Chaney, Ralph W., article, 145-151
Chapman, John A., article, 41-49
Chitty, Dennis, article, 227-237
Chlorella vulgaris, alga, as food for *Daphnia*, 522
Choristoneura fumiferana, spruce budworm, recurrent infestations of, 62
Circulation in estuaries, 191
Cirsium undulatum, thistle, use of P^{32} in tracing some insect-plant relationships of, 187
Clam, hard, fed upon by mud crab, 422
Clark, Philip J., article, 445-453
Clearing, forest, in southeastern Queensland, soil mantle movement in relation to, 380
Clements, Frederic E., and his concepts in ecology, a tribute to, 114
Clements, Frederic E., as I knew him, 112
Clements, Frederic E., biography, 109-112
Clements, Frederic E., Memorial at A. and M. College of Texas, 116

Clements, Frederic E., photograph of, 108
Climates of the Great Smoky Mountains, article, 354-361
Climax vegetation and the regional shift of controls, note, 575-579
Coaldrake, J. E., co-author, article, 380-388
Cole, LaMont C., review, 589
Collembola feeding upon nematodes, note, 421
Colorado, analysis of juniper-pinyon of, 473
Communities, flood-plain, of lower Mississippi valley, 126
Communities, history and evaluation of various concepts of, 152
Communities, plant, soil phosphate and delimitation of, 370
Community, spruce-fir, on Kaibab Plateau, Arizona, analysis of, 316
Comparison of line interception and point contact methods in the analysis of mixed grass range vegetation, article, 431-436
Competition as a possible limiting factor in the distribution of *Microtus*, note, 418-420
Concepts of communities, 152
Continental divide, juniper-pinyon east of the, analyzed, 473
Contribution to the theory of the living organism, a, reviewed, 99-100
Controls, climax vegetation and the regional shift of, 575
Coregonus nasus, whitefish, mortality rates of, 388
Costin, A. B., note, 580
Crab, mud, feeding upon hard clams, 422
Crassostrea virginica, oyster, factors controlling distribution of, 322
Crawfish, American, introductions into foreign lands, 296
Crayfish, distribution of, 573
Cretaceous of Minnesota, a new pine from, 145
Curry, La Verne L., article, 541-550

D

Dansereau, Pierre, note, 575-579; review, 589-590
Daphnia magna, cladoceran, affected by its phytoplankton food source, 522
Davies, R., co-author, reviewed, 587-588
Dawson, William R., co-author, articles, 181-187, 466-472
DeLacy, Allan C., and Thomas S. English, article, 18-20
Density of population, effect on oviposition rate, 253
Der Zeitfaktor in Geologie und Paläontologie, reviewed, 428
Desert bird, mourning dove, temperature and water adaptations of, 181
Dexter, Ralph W., and Edward C. Kinney, note, 289
Dice, Lee R., review, 301-302
Die Binnengewässer. Vol. 20. Chironomus, reviewed, 425-426
Die-off, cattail, experiment to prevent, 418
Diptera, midges, ecology of, 541
Diptera as summit-frequenting insects, 41, 50
Dispersal, long-distance, 569
Distance to nearest neighbor as a measure of spatial relationships in populations, article, 445-453
Distribution of crayfish, 573
Distribution of oysters in a neutral estuary, 322
Dodge, Harold R., and John M. Seago, article, 50-59
Dowdeswell, W. H., reviewed, 301
Downs and dunes: their plant life and its environment, reviewed, 302-304
Dreyer, William A., review, 588
Drift lines, maritime, ecology of spiders of, 25
Duncan, Donald P., article, 498-521
Dune and downland autecology and ecosystems, review, 302-304
Dyksterhuis, E. J., review, 426

E

Early view of the relation between plant distribution and environmental factors, note, 97-98
Earth's cover of vegetation, place of grasslands in, 143
Earthworm, *Sparganophilus eiseni*, recorded in western Lake Erie, 289
Ecological distribution of the *Peromyscus leucopus* species group in eastern Texas, article, 375-379
Ecological studies of forest trees at Chalk River, Ontario, Canada. I. Tree species in relation to soil moisture sites, article, 406-414
Ecology and taxonomy, parallelisms between, 92
Ecology, animal, role of thermal radiation in, 562
Ecology—an initiation, review, 297-298
Ecology, hexicology: a note for the history of, 415
Ecology of midge fauna of a Michigan creek, 541
Ecology of serpentine soils, symposium, 258-288
Ecology of species of *Megachile* Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa, article, 453-462
Ecology of the Opuntiae in the Big Bend region of Texas, article, 334-347
Ecology of the spiders of maritime drift lines, article, 25-35
Effects of moderate grazing on the composition and plant production of a native tall-grass prairie in central Oklahoma, article, 200-207
Effects of saturated soil on seedling growth of some bottomland hardwood species, article, 36-41
Egler, Frank E., reviews, 99-100, 424-425
Ellison, Lincoln, article, 380-388
Emerson, Alfred E., reviews, 102-103, 428
English text on animal ecology, review, 301
English, Thomas S., co-author, article, 18-20
Enlargement of the bay lakes of North Carolina, evidence for, 78
Entomophagous insects under mass culture, 245
Environmental factors and plant distribution, 97
Epizootics in wild voles, 227
Equations descriptive of fish schools and other animal aggregations, article, 361-370
Establishment and food habits of the nutria in Texas, article, 172-176
Estuaries, relation between circulation and planktonic populations in, 191
Estuary, distribution of oysters in an, 322
Evaluation and history of various concepts of plant and animal communities in North America, article, 152-171
Evans, Francis C., co-author, article, 445-453
Evaporation from a clay loam soil, influence of pine shade and litter on, 397
Evaporation rate, related to vapor pressure and wind, 71
Everhart, W. H., co-author, reviewed, 104
Evidence of four pine species from fossil pollen in Michigan, article, 327-331
Example of long distance dispersal, article, 569-572
Experiment to prevent cattail die-off, 418
Explanation for the distribution of a North American crayfish, note, 573-575

F

Factors affecting natural regeneration of tamarack, 498
Factors affecting plant growth on serpentine soils, article, 259-266
Factors controlling the distribution of oysters in a neutral estuary, article, 322-327

Fauna of tree-hole complex, 208
Fecundity of entomophagous insects under mass culture, an effect of environmental resistance, article, 245-249
Feeding of *Daphnia*, 522
Findley, James S., note, 418-420
Fire, related to forests of Itasca in nineteenth century, 21
First Book of Ecology, reviewed, 588
Fischer, A. G., co-author, reviewed, 423
Fish, bluegills, food turnover of population of, 490
Fish, game, in a flood-control reservoir, 305
Fish, seining methods for, 18
Fish, whitefish, mortality rates of in Arctic lake, 388
Fish mortality and river pollution, 580
Fish schools, equations describing, 361
Fishery science: its methods and applications, reviewed, 104
Fishes, marine, in fresh and brackish river waters, 75
Flanders, Stanley E., articles, 245-249, 292-293
Flood plain biotic communities of lower Mississippi Valley, 126
Florida, factors controlling distribution of oysters in an estuary in, 322
Food habits of nutria, 172
Food supply, limited, effect on unconfined house-mouse population, 249
Food turnover of a bluegill population, article, 490-498
Forage production on longleaf pine lands of southern Alabama, article, 59-62
Forest lowland, as habitat of *Peromyscus leucopus* in eastern Texas, 375
Forest, upland, as habitat of *Peromyscus gossypinus* in eastern Texas, 375
Forest, upland, survey of, in Milwaukee area, 533
Forest clearing in southeastern Queensland, soil mantle movement in relation to, 380
Forests of Itasca in the nineteenth century as related to fire, article, 21-25
Forest trees at Chalk River, Ontario, ecological studies of, 406
Forest types, Appalachian, plotless sampling trials in, 237
Foreword to Frederic E. Clements Memorial Issue, 107
Fossil pollen in Michigan, evidence of four pine species from, 327
Fothergill, Philip G., reviewed, 302
Frank, Peter W., review, 297-298
Fraser, Donald A., article, 406-414
Fraser River Valley, British Columbia, survival of plants under flood in, 94
Fresh-water invertebrates of the United States, reviewed, 300-301
Frey, David G., article, 78-88
Fujita, Hiroshi, article, 253-257
Fundamentals of Ecology, reviewed, 297, 297-298
Further study of the tree-hole complex with emphasis on quantitative aspects of the fauna, 208-222

G

Gaines, E. N., article, 59-62
Gale, E. P., co-author, reviewed, 587-588
Geiger-Müller counter, used for tracing field voles, 5
Geologic time and evolution, review, 428
Georgia, summit-frequenting Diptera in, 50
Gerking, Shelby D., article, 490-498
Gerloff, Gerald C., and Folke Skoog, article, 348-353
Gilbert, Perry W., review, 104
Giltz, M. L., note, 418
Godfrey, Gillian K., article, 5-10
Gorham, Eville, note, 97-98
Graham, Ben F., Jr., note, 415
Grange, Wallace Byron, reviewed, 301-302
Grasslands in the earth's cover of vegetation, place of, 143
Grass range vegetation, methods in the analysis of, 431
Gray, James, reviewed, 104
Grayson, John F., article, 327-331
Grazing, moderate, effects of on the composition and plant production of prairie, 200
Great Smoky Mountains, climates of, 354
Growth, plant, on serpentine soils, 259
Growth, seedling, of bottomland hardwood species, 36
Growth and differentiation in plants, reviewed, 427-428
Growth of algal cells, 348
Growth rates of regal horned lizard, 420
Gruber, Jacob W., note, 415-417
Grundmann, Albert W., co-author, article, 187-191
Gulls, young, temperature regulation in, 466

H

Hamilton, W. J., Jr., review, 426-427
Hanson, Herbert C., foreword to Clements Memorial Issue, 107
Hardwood species, bottomland, effects of saturated soil on seedling growth of, 36
Hardy's "animal exclusion" theory, 522
Heat balance of mammals, 562
Heitman, Hubert, Jr., co-author, note, 562-569
Henson, E. B., note, 579
Herd of mule deer, reviewed, 426-427
Herons, young, temperature regulation in, 466
Hexicology: a note for the history of ecology, note, 415-417
Hickox, J. E., co-author, reviewed, 423
Hirst, L. Fabian, reviewed, 589
Historical aspects of organic evolution, reviewed, 302
History and evaluation of various concepts of plant and animal communities in North America, article, 152-171
History of ecology, hexicology, 415
Hobbs, G. A., and C. E. Lilly, article, 453-462
Homeothermy, development of, in birds, 466
House-mouse population, unconfined, effect of limited food supply on, 249
How animals move, reviewed, 104
Huffman, Roy E., reviewed, 426
Husch, Bertram, article, 11-17
Hydrobiology of Atwood Lake, a flood-control reservoir, article, 305-316

I

Infestations, recurrent, of spruce budworm in Ontario, 62
Influence of shade and litter of pine on evaporation from a clay loam soil at Berkeley, California, article, 397-405
Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction, and survival, article, 522
Insect-plant relationships of the thistle, 187
Insect physiology, reviewed, 298-300
Insects, entomophagous, under mass culture, 245
Insects, summit-frequenting, 41, 50
Interpretation of the changes in type of the population density effect upon the oviposition rate, an, article, 253-257
Introduction, the ecology of serpentine soils, symposium, 258-259
Introductions of American crawfish into foreign lands, note, 296
Irrigation development and public water policy, reviewed, 426

Islands of Basswood Lake, Minnesota, small mammal populations of, 437
Isotopes, radiactive, into tree stems, a technique for introducing, 415
Isotopes, radioactive, used in studying insect-plant relationships, 187
Isotopes, radioactive, used in tracing voles, 5
Itasca, forests of, as related to fire, 21

J

Jackson, Daniel F., and James McFadden, article, 1-4
Jensen, Paul, review, 302
Johannsen, O. A., review, 425-426
Juniper-pinyon east of the continental divide as analyzed by the line-strip method, article, 473-489

K

Kaibab Plateau, Arizona, spruce-fir community on, 316
Kelly, C. F., T. E. Bond, and Hubert Heitman, Jr., note, 562-569
Kelting, Ralph W., article, 200-207
Kendeigh, S. Charles, article, 152-171
Ketchum, Bostwick H., article, 191-200
Kinney, Edward C., co-author, note, 289
Kittredge, Joseph, article, 397-405
Kruckleberg, A. R., article, 267-274
Kucera, C. L., article, 71-75

L

Lac Seul area of northwestern Ontario, recurrent infestations of spruce budworm in, 62
Lake Erie, earthworm recorded from, 289
Lake Erie, western, phytoplankton and turbidity in, 550
Lake Vyrnwy, Montgomeryshire, voles in area of, 227
Lakes, bay, Carolina: the bog margin problem, 584
Lakes, bay, of North Carolina, evidence for recent enlargement of, 78
Landers, Warren S., note, 422
Larix laricina, tamarack, factors affecting natural regeneration of, 498
Larus occidentalis livens, western gull, temperature regulation in young of, 466
Laucks, Irving F., reviewed, 424-425
Lepomis macrochirus, bluegill, food turnover of population of, 490
Leucichthys sardinella, whitefish, mortality rates of, 388
Lilly, C. E., co-author, article, 453-462
Lindsey, Alton A., co-author, article, 473-489
Line interception and point contact methods in the analysis of mixed grass range vegetation, comparison of, 431
Line-strip method, juniper-pinyon east of continental divide analyzed by, 473
Linsdale, Jean M., and P. Quentin Tomich, reviewed, 426-427
Linsley, E. G., co-author, reviewed, 102-103
Litter and shade of pine, influence of on evaporation from soil, 397
Lizard, regal horned, field movements and growth rates of, 420
Long distance dispersal, example of, 569
Longleaf pine lands, forage production on, 59
Loomis, W. E. (editor), reviewed, 427-428
Lowe, Charles H., Jr., note, 420-421
Lukens, Paul, co-author, article, 437-447

M

Macquarie Island, Australia, an example of long distance dispersal, 569
Mammalian populations of lake islands, 437
Marine fishes in fresh and brackish waters of Virginia rivers, article, 75-78
Marshall, Nelson, article, 322-327
Mass culture of entomophagous insects, 245
Massman, William H., article, 75-78
Mating of flies on mountain summits, 50
Mayfly nymph, occurrence of, in brackish water, 98
Mayr, E., E. G. Linsley, and R. L. Usinger, reviewed, 102-103
McCarley, W. H., article, 375-379
McDermott, R. E., article, 36-41
McFadden, James, co-author, article, 1-4
McMillan, Calvin, note, 92-94
Measure of spatial relationships in populations, distance to nearest neighbor as a, 445
Megachile, bee, ecology of in southern Alberta, 453
Merkle, John, article, 316-322
Method for study of interacting host-parasite populations, 292
Methods, in analysis of mixed grass range vegetation, comparison of, 431
Methods and principles of systematic zoology, reviewed, 102-103
Mice, *Peromyscus,* ecological distribution of, in eastern Texas, 375
Mice on islands of a Minnesota lake, 437
Michigan, evidence of four pine species from fossil pollen in, 327
Michigan, Hunt Creek, ecology of midge fauna of, 541
Microclimate of the tree-hole, 208
Microcystis aeruginosa, alga, nitrogen and phosphorus in cells of, 348
Microtus agrestis, field vole, tuberculosis in, 227
Microtus agrestis, field vole, use of Geiger-Müller counter in tracing, 5
Microtus spp., voles, competition as a possible limiting factor in distribution of, 418
Midge fauna of a Michigan Creek, ecology of, 541
Milwaukee area, an upland forest survey of the, 533
Minnesota, a new pine from the Cretaceous of, 145
Minnesota, Basswood Lake, mammalian populations on islands of, 437
Minnesota, factors affecting natural regeneration of tamarack in, 498
Minnesota, forests of Itasca in the nineteenth century as related to fire, 21
Missouri, some relationships of evaporation rate to vapor pressure deficit and low wind velocity in, 71
Mississippi Valley, lower, flood plain biotic communities of, 126
Moisture sites, soil, tree species in relation to, 406
Monograph on chironomids, review, 425-426
Montana, western, summit-frequenting insects in, 41
Moore, P. G., article, 222-227
Morrison, P., review, 587-588
Mortality, fish, and river pollution, observations on, 580
Mortality among wild voles, infectious disease as a cause of, 227
Mortality rates of whitefish in an arctic lake, article, 388-396
Moul, Edwin T., review, 297
Mountain-summit insects, 41, 50
Mountains, Great Smoky, climates of, 354
Mourning dove, body temperature and water requirements of, 181
Movement, soil mantle, in relation to forest clearing, 380
Muscidae, Diptera, on Georgia mountain summits, 50

Mus musculus, house-mouse, effect of limited food supply on unconfined population of, 249
Myocastor coypu, nutria, establishment in Texas and food habits of, 172
Myser, W. C., co-author, note, 418

N

Natural regeneration of tamarack, factors affecting, 498
Nature and place of transition from true prairie to mixed prairie, article, 117-126
Nebraska, nature and place of transition from true prairie to mixed prairie in, 117
Neill, Wilfred T., and E. Ross Allen, note, 581-584
Nematodes, as food for Collembola, 421
Neopanope texana, mud crab, preying upon hard clam, 422
New ecology text book, review, 297
Newell, N. D., J. K. Rigby, A. G. Fischer, A. J. Whiteman, J. E. Hickox, and J. S. Bradley, reviewed, 423
New Jersey, *Carex kobomugi* at Island Beach, 289
New Mexico, juniper-pinyon east of the continental divide as analyzed by the line-strip method, 473
New omnium gatherum of paleozoology, review, 100-102
New pine from the Cretaceous of Minnesota and its paleoecological significance, article, 145-151
New Textbook of Geology, reviewed, 589-590
Nitrogen in algal cells, as a measure of its availability for growth, 348
Normal field movements and growth rates of marked regal horned lizards (*Phrynosoma solare*), note, 420-421
North America, history and evaluation of various concepts of plant and animal communities in, 152
North American Prairie, reviewed, 591
North Carolina, bottomland hardwood species, seedling growth of, 36
North Carolina bay lakes: the bog margin problem, 78, 584
North Carolina, climates of the Great Smoky Mountains, 354
North Dakota, comparison of two methods in analysis of mixed grass range vegetation, 431
Notes on the ecology of the midge fauna (Diptera: Tendipedidae) of Hunt Creek, Montmorency County, Michigan, article, 541-550
Notes on the predation of the hard clam, *Venus mercenaria,* by the mud crab, *Neopanope texana,* note, 422
Nutria, in Texas, 172

O

Occurrence of a mayfly nypmph in brackish water, note, 98
Odum, Eugene P., reviewed, 297, 297-298
Ohio, hydrobiology of Atwood Lake in, 305
Ohio, phytoplankton and turbidity in western Lake Erie, 550
Oklahoma, effects of moderate grazing on native tall-grass prairie in, 200
Oklahoma, plant succession and yield of living plant material in a plowed prairie in, 176
Olson, David, co-author, article, 437-445
Olson, Jerry S., review, 302-304
Ontario, ecological studies of forest trees at Chalk River, 406
Ontario, northwestern, recurrent spruce budworm infestations in, 62
Opuntiae in Texas, ecology of, 334
Orconectes neglectus neglectus, crayfish, distribution of, 573
Oregon, vegetational response to serpentine soils, 275
Orr, Howard D., article, 332-334
Oviposition rate in insects, population density effect on, 253
Oysters, distribution of, in a neutral estuary, 322

P

P^{32}, use of, in tracing some insect-plant relationships of the thistle, 187
Parallelisms between ecology and taxonomy, note, 92-94
Park, Orlando, and Stanley Auerbach, article, 208-222
Pelecanus occidentalis californicus, brown pelican, temperature regulation in young of, 466
Pendleton, Robert C., article, 187-191
Penfound, Wm. T., co-author, article, 176-180
Penn, George Henry, note, 296
Pennak, R. W., reviewed, 300-301
Pennsylvania, northwestern, regeneration of *Prunus serotina* in, 11
Pennsylvania, phytoplankton photosynthesis in Sanctuary Lake, Pymatuning Reservoir, 1
Permian marine paleoecology, review, 423
Permian reef complex of the Guadalupe Mountains region, Texas and New Mexico, reviewed, 423
Peromyscus leucopus species group, mice, ecological distribution of, in eastern Texas, 375
Petrides, George A., co-author, article, 172-176
pH of soils: facts and fallacies, note, 89-92
Phillips, John, article, 114-115
Phosphate, soil, and the delimitation of plant communities in eastern Australia, 370
Phosphorus in algal cells, as a measure of its availability for growth, 348
Photosynthesis, phytoplanktonic, in Sanctuary Lake, 1
Phrynosoma solare, regal horned lizard, filed movements and growth rates of, 420
Physiological inhibition of *Daphnia* cultures by algae, 522
Phytoplankton and turbidity in western Lake Erie, 550-561
Phytoplankton photosynthesis in Sanctuary Lake, Pymatuning Reservoir, article, 1-4
Phytoplankton populations of Atwood Lake, a flood-control reservoir, 305
Phytoplankton populations, inhibitory effects of on *Daphnia,* 522
Pine lands, longleaf, of southern Alabama, forage production on, 59
Pine, new, from the Cretaceous of Minnesota, 145
Pine species from fossil pollen in Michigan, 327
Pine, influence of shade and litter of, on soil evaporation, 397
Pinyon-juniper east of the continental divide, as analyzed by the line-strip method, article, 473-489
Piveteau, Jean (editor), reviewed, 100-102
Place of grasslands in the earth's cover of vegetation, article, 143-145
Plague—An Ancient and Persisting Ecological Problem, reviewed, 589
Planktonic populations in estuaries, 191
Plant distribution and environmental factors, 97
Plant growth on serpentine soils, factors affecting, 259
Plant-insect relationships of the thistle, 187
Plant material, living, yield of, and plant succession in a plowed prairie, 176
Plant populations, spacing in, 222
Plant production and composition of tall-grass prairie, effects of grazing on, 200
Plant species in relation to serpentine soils, article, 267-274

Plant succession and yield of living plant material in a plowed prairie in central Oklahoma, article, 176-180
Plants, survival of, under flood, 94
Plotless sampling trials in Appalachian forest types, article, 237-244
Plowed prairie in central Oklahoma, plant succession and yield in, 176
Point Barrow, Alaska, lake near, mortality rates of whitefish, in, 388
Point contact methods in analysis of vegetation, comparison of line interception and, 431
Pollen, fossil, pine species from, 327
Pollen study of two bogs in Texas, article, 462-466
Pollination of alfalfa and bees, 453
Pollution as a factor in protozoan production of a lake, 332
Pollution, river, and fish mortality, 580
Pontoporeia affinia var. *brevicornis* in Cayuga Lake, N. Y., note, 579
Pool, Raymond J., article, 109-112
Population, bluegill, food turnover of, 490
Population density, effect on oviposition rate, 253
Populations, *Daphnia,* affected by phytoplankton, 522
Populations, distance to nearest neighbor as a measure of spatial relationships in, 445
Populations, host-parasite, method for study of, 292
Populations, house-mouse, unconfined, effect of limited food supply on, 249
Populations, mammalian, of lake islands, 437
Populations, planktonic, in estuaries, 191
Populations, plant, spacing in, 222
Populations of entomophagous insects, fecundity in, 245
Populations of whitefish, mortality rates in, 388
Potzger, J. E., article, 462-466
Pound, Roscoe, article, 112-113
Prairie, nature and place of transition from mixed to true, 117
Prairie, plowed, plant succession and yield of living material in, 176
Prairie, tall-grass, effects of moderate grazing on, 200
Predation as a factor in oyster distribution, 322
Predation of Collembola upon nematodes, 421
Predation of mud crabs on the hard clam, 422
Principles of General Ecology, reviewed, 585-587
Production of forage on longleaf pine lands, 59
Productivity of a flood-control reservoir, 305
Protein turnover of a bluegill population, 490
Protozoa of the tree-hole complex, 208
Protozoan populations of a Pennsylvania lake, 332
Prunus serotina, black cherry, regeneration following cutting, 11
Puget Sound, beach seining at, 18
Pymatuning Reservoir, phytoplankton photosynthesis in, 1
Pymatuning Reservoir, protozoan populations of, 332

Q

Quantitative studies of protozoan populations from two areas of Pymatuning Lake, Pennsylvania, article, 332-334
Queensland, southeastern, soil mantle movement in relation to forest clearing in, 380

R

Radiation, solar, and temperatures of young birds, 466
Radiation, thermal, role of in animal ecology, 562
Radioactive isotopes, technique for introducing into tree stems, 415
Range of field voles, studied with Geiger counter, 5
Range vegetation, comparison of methods in the analysis of, 431
Reaction of soils: fact and fallacies, note, 89-92
Record of the earthworm, *Sparganophilus eiseni,* from the basin of western Lake Erie, 289
Recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario, article, 62-71
Regeneration, natural, of tamarack, factors affecting, 498
Regeneration of *Prunus serotina* in northwestern Pennsylvania following cutting, article, 11-17
Regional shift of controls, climax vegetation and, 575
Regulatory mechanisms in house-mouse populations: the effect of limited food supply on an unconfined population, article, 249-253
Relation between circulation and planktonic populations in estuaries, article, 191-200
Relation between plant distribution and environmental factors, an early view of, 97
Relation of systematics to other fields, review, 102-103
Relationships of evaporation rate to vapor pressure deficit and low wind velocity, article, 71-75
Response, vegetational, to serpentine soils, 275
Rice, Elroy L., article, 176-180
Richards, O. W., reviewed, 428
Ricker, W. E., review, 104
Rigby, J. K., co-author, reviewed, 423
River pollution and fish mortality, 580
Roeder, K. D., reviewed, 298-300
Role of thermal radiation in animal ecology, note, 562-569
Roots, lateral, a note on the grouping of, 293
Rounsefell, G. A., and W. H. Everhart, reviewed, 104
Ryther, John H., article, 522-533

S

Salamun, Peter J., co-author, article, 533-540
Salisbury, Sir Edward, reviewed, 302-304
Samples, beach seine, variations in, 18
Sampling trials, plotless, in Appalachian forest types, 237
Sanctuary Lake, Pymatuning Reservoir, phytoplankton photosynthesis in, 1
Sarcophagidae and other Diptera taken by trap and net on Georgia mountain summits in 1952, article, 50-59
Saturated soil, effects of, on seedling growth of hardwoods, 36
Schindewolf, O. H., reviewed, 428
Schneiderman, H. A., review, 298-300
Schools, fish, equations describing, 361
Seago, John M., co-author, article, 50-59
Seedling growth of bottomland hardwood species, effects of saturated soil on, 36
Seine samples, beach, variations in, 18
Serpentine soils, factors affecting plant growth on, 259
Serpentine soils, plant species in relation to, 267
Serpentine soils, the ecology of, symposium, 258-288
Serpentine soils, vegetational response to, 275
Shade and litter of pine, influence of, on soil evaporation, 397
Shanks, Royal E., articles, 237-244, 354-361
Shantz, H. L., article, 143-145
Shelford, V. E., article, 126-142
Shrews on islands of a Minnesota lake, 437
Siggeirsson, Einar I., co-author, article, 431-436
Simplified method for the study of interacting host-parasite populations, note, 292-293
Sites, tree species in relation to soil moisture, 406
Sitotroga cerealella, grain moth, culture of, 292
Skoog, Folke, co-author, article, 348-353

Sloan, William C., co-author, note, 98
Small, John A., note, 289-291
Small mammal populations on the islands of Basswood Lake, Minnesota, article, 437-445
Social insects, reviewed, 428
Soil, clay loam, influence of shade and litter of pine on evaporation from, 397
Soil mantle movement in relation to forest clearing in southeastern Queensland, article, 380-388
Soil moisture sites, tree species in relation to, 406
Soil phosphate and the delimitation of plant communities in eastern Australia, article, 370-275
Soils, reaction of, facts and fallacies, 89
Soil, saturated, effects of, on hardwood seedling growth, 36
Soils, serpentine, plant growth on, 259
Soils, serpentine, plant species in relation to, 267
Soils, serpentine, ecology of, 258
Soils, serpentine, vegetational response to, 275
Spacing in plant populations, article, 222-227
Sparganophilus eiseni, earthworm, recorded in western Lake Erie, 289
Spatial relationships in populations, 445
Species, plant, in relation to serpentine soils, 267
Speculation in reality, reviewed, 424-425
Spiders of maritime drift lines, ecology of, 25
Spruce budworm infestations in northwestern Ontario, 62
Spruce-fir community on the Kaibab Plateau, Arizona, 316
Spurr, Stephen H., article, 21-25
Steward, F. C., review, 427-428
Storer, John H., reviewed, 588
Strecker, Robert L., article, 249-253
Studies on summit-frequenting insects in western Montana, article, 41-49
Succession, plant, and yield of living plant material in plowed prairie, 176
Summit-frequenting insects, 41, 50
Survey, upland forest, of Milwaukee area, 533
Survival of plants under flood, 94
Swank, Wendell G., and George A. Petrides, article, 172-176
Symposium: the ecology of serpentine soils, 258-288

T

Tall-grass prairie, effects of grazing on, 200
Tamarack, factors affecting natural regeneration of, 498
Taxonomy and ecology, parallelisms between, 92
Taylor, B. W., article, 569-572
Technique for introducing radioactive isotopes into tree stems, note, 415
Temperature, body, of mourning dove, 181
Temperature regulation in young pelicans, herons, and gulls, article, 466-472
Tennessee, climates of the Great Smoky Mountains, 354
Tennessee, plotless sampling trials in forest types, 237
Texas, distribution of mice in, 375
Texas, ecology of cacti in, 334
Texas, analysis of juniper-pinyon of, 473
Texas, nutria in, 172
Texas, pollen study of two bogs in, 462
Tharp, B. C., co-author, article, 462-466
Thienemann, August, reviewed, 425-426
Thistle, *Cirsium undulatum,* insect relationships of, 187
Those of the forest, reviewed, 301-302
Tomich, P. Quentin, reviewed, 426-427
Toxoplasma, protozoan parasite, in wild voles, 227
Tracing field voles (*Microtus agrestis*) with a Geiger-Müller counter, article, 5-10
Traité de paléontologie, T. I, II, III, reviewed, 100-102
Transition from true prairie to mixed prairie, nature and place of, 117
Tree-hole complex, fauna of, 208
Tree species in relation to soil moisture sites, article, 406-414
Tree stems, technique for introducing radioactive isotopes into, 415
Trichogramma sp., chalcid flies, culture of, 292
Tuberculosis among wild voles: with a discussion of other pathological conditions among certain mammals and birds, article, 227-237
Turbidity in western Lake Erie and phytoplankton, 550
Turtles, algae on, 581

U

Universe, experimental, 292
Upland forest survey of the Milwaukee area, article, 533-540
Usinger, R. L., co-author, reviewed, 102-103

V

Vallentyne, J. R., review, 301
Vapor pressure and wind velocity, relationships to evaporation rate, 71
Variations in beach seine samples caused by net length and repeated hauls, article, 18-20
Vegetation, climax, 575
Vegetation, place of grassland in, 143
Vegetation, range, comparison of methods in analysis of, 431
Vegetation of Texas ponds, affected by nutria, 172
Vegetational response to serpentine soils, article, 275-288
Venus mercenaria, hard clam, preyed upon by mud crab, 422
Verduin, Jacob, article, 550-561
Virginia rivers, marine fishes in, 75
Vole, use of Geiger-Müller counter in tracing, 5
Voles, tuberculosis among, 227
Von Engeln, O. D., co-author, reviewed, 589-590

W

Walker, R. B., article, 259-266
Water requirements of the mourning dove, 181
Weaver, J. E., article, 117-126; reviewed, 591
Wells, B. W., note, 584
Wells, John W., reviews, 100-102, 423, 428
Whitefish, mortality of, in an arctic lake, 388
Whiteman, A. J., co-author, reviewed, 423
Whitford, Philip B., article, 533-540
Whitman, Warren C., article, 431-436
Whittaker, R. H., articles, 258-259, 275-288
Wilds, S. A., note, 89-92
Williams, Austin B., note, 573-575
Wind velocity and vapor pressure, relationships with evaporation rate, 71
Wisconsin, upland forest survey in, 533
Wohlschlag, Donald E., article, 388-396
Woodbury, Angus M., reviewed, 585-587
Woodin, Howard E., article, 473-489
Wright, John C., article, 305-316

Y

Yield of living plant material and plant succession in a plowed prairie in central Oklahoma, article, 176-180
Young, Vernon A., article, 116

Z

Zenaidura macroura marginella, mourning dove, body temperature and water requirements in, 181
Zooplankton of a flood-control reservoir, 305